Revision and new data of the ammonite family Pseudotissotiidae in the Iberian Trough, Spain

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Revisión y nuevos datos de la familia de ammonites Pseudotissotiidae en el Surco Ibérico, España

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Abstract

The ammonites assigned to the family Pseudotissotiidae of the Wiedmann (Tübingen, Germany) and Goy, Carretero and Meléndez (Madrid, Spain) collections obtained from the Iberian Trough have been revised. New, mainly lower Turonian, specimens of the species *Pseudotissotia* sp., *Choffaticeras (Choffaticeras) quaasi* (Peron, 1904), *C. (C.) pavillieri* (Pervinquière, 1907), *C. (C.) segne* (Solger, 1903), *C. (C.) sinaiticum* (Douvillé, 1928), *C. (Leoniceras) luciae* (Pervinquière, 1907), *C. (L.) barjonai* (Choffat, 1898), *Wrightoceras llarenai* (Karrenberg, 1935), *W. munieri* (Pervinquière, 1907), *W. submunieri* Wiedmann, 1975b, and *Donenriquoceras forbesiceratiforme* Wiedmann, 1960, have been also presented. In addition, we designate and refigure the lectotype of *Pseudotissotia (Leoniceras) alaouitense* Basse, 1937, and refigure the lectotype of *P. barjonai* Choffat, 1898. Studies on the morphologies and the geographical and temporal distributions of all of these species have led to the identification of several phylogenetic relationships between them, and to distinguish four main phases in the evolution of the family, characterized by the successive dominance of *Choffaticeras (Choffaticeras)*, *Choffaticeras (Leoniceras)*, *Donenriquoceras* and *Wrightoceras* with *Donenriquoceras*.

Résumé

Ce travail présente une révision des ammonites des collections Wiedmann (Tübingen, Allemagne) et Goy, Carretero et Meléndez (Madrid, Espagne) qui proviennent du Bassin Ibérique et qui ont été assignées à la famille des Pseudotissotiidae. Sont également présentés de nouveaux exemplaires, majoritairement du Turonien inférieur, de *Pseudotissotia* sp., *Choffaticeras (Choffaticeras) quaasi* (Peron, 1904), *C. (C.) pavillieri* (Pervinquière, 1907), *C. (C.) segne* (Solger, 1903), *C. (C.) sinaiticum* (Douvillé, 1928), *C. (Leoniceras) luciae* (Pervinquière, 1907), *C. (L.) barjonai* (Choffat, 1898), *Wrightoceras llarenai* (Karrenberg, 1935), *W. munieri* (Pervinquière, 1907), *W. submunieri* Wiedmann, 1975b, et *Donenriquoceras forbesiceratiforme* Wiedmann, 1960. Le lectotype de *Pseudotissotia (Leoniceras) alaouitense* Basse, 1937, est désigné et refiguré, et le lectotype de *P. barjonai* Choffat, 1898, est refiguré dans ce travail. L'étude morphologique et les distributions géographiques et temporelles de ces espèces ont permis de les situer d'un point de vue phylogénétique et de distinguer quatre étapes principales dans l'évolution de la famille caractérisées par la dominance successive de *Choffaticeras (Choffaticeras)*, *Choffaticeras (Leoniceras)*, *Donenriquoceras* et *Wrightoceras* avec *Donenriquoceras*.

Resumen

En este trabajo se ha desarrollado una revisión de los ammonites de las colecciones Wiedmann (Tübingen, Alemania) y Goy, Carretero y Meléndez (Madrid, España) procedentes del Surco Ibérico y asignados a la familia Pseudotissotiidae. Se han presentado nuevos ejemplares, en su mayoría del

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Turoniense inferior, atribuidos a *Pseudotissotia* sp., *Choffaticeras (Choffaticeras) quaasi* (Peron, 1904), *C. (C.) pavillieri* (Pervinquière, 1907), *C. (C.) segne* (Solger, 1903), *C. (C.) sinaiticum* (Douvillé, 1928), *C. (Leoniceras) luciae* (Pervinquière, 1907), *C. (L.) barjonai* (Choffat, 1898), *Wrightoceras llarenai* (Karrenberg, 1935), *W. munieri* (Pervinquière, 1907), *W. submunieri* Wiedmann, 1975b, y *Donenriquoceras forbesiceratiforme* Wiedmann, 1960. Igualmente, se ha designado y refigurado el lectotipo de *Pseudotissotia (Leoniceras) alaouitense* Basse, 1937, y refigurado el lectotipo de *P. barjonai* Choffat, 1898. El estudio de las morfologías y las distribuciones geográficas y temporales de estas especies ha permitido la identificación de varias líneas filogenéticas y de cuatro etapas principales en la evolución de la familia, caracterizadas por el dominio sucesivo de *Choffaticeras (Choffaticeras)*, *Choffaticeras (Leoniceras)*, *Donenriquoceras* y *Wrightoceras* con *Donenriquoceras*.

Keywords: Upper Cenomanian; Lower Turonian; Ammonoidea; Pseudotissotiidae; Iberian Trough; Spain

Mots clés : Cénomanien supérieur ; Turonien inférieur ; Ammonoidea ; Pseudotissotiidae ; Bassin Ibérique ; Espagne

Palabras clave : Cenomaniense superior; Turoniense inferior; Pseudotissotiidae; Surco Ibérico; España

1. Introduction

This paper first presents a revision of ammonites assigned to the family Pseudotissotiidae Hyatt, 1903, from the Iberian Trough that are currently held in the Institut und Museum für Geologie und Paläontologie (GPI), Tübingen, Germany and the Universidad Complutense de Madrid (UCM), Madrid, Spain. These centres hold the Wiedmann, Goy, Carretero and Meléndez palaeontological collections, which include most of the Pseudotissotiidae specimens from the mentioned palaeogeographical region. Subsequently, a detailed taxonomic analysis has been made of the members of this family obtained during fieldwork carried out for this investigation. The fieldwork took place in the upper Cenomanian and lower Turonian outcrops situated in the localities of Puentedey and Soncillo, in the north of the province of Burgos, of Fuentetoba, in the centre of Soria, and of Cantalojas, Galve de Sorbe, Condemios, Somolinos and Tamajón, in the north of Guadalajara, Spain (Fig. 1). Finally, the information obtained has made it possible to reach several conclusions concerning the taxonomy, distribution and evolution of the pseudotissotiids.

In order to establish a more precise systematic classification of the taxa being dealt with, the first author has also studied the original types attributed to this family that are held in the Museu do Instituto Geológico e Mineiro of Lisboa, Portugal, and in the Musée National d'Histoire Naturelle of Paris, France.

Fig. 1. Geographic provenance of the specimens presented in this paper.
Fig. 1. Origine géographique des spécimens présentés dans ce papier.

From a stratigraphical point of view, the ammonites presented herein have been mainly collected from the Margas de Puentedey (Floquet et al., 1982) and Margas de Picofrentes (Floquet et al., 1982) formations, deposited respectively in the inner and in the marginal environments of the platform. These formations are remarkable for containing the most complete and characteristic marls of the studied interval in the entire north and centre of Spain, as pointed out by Wiedmann (1960, 1964, 1975a, 1975b, 1979), Wiedmann and Kauffman (1978), Floquet et al. (1982), Floquet (1991), Santamaría-Zabala (1991, 1992, 1995) and Segura et al. (1993), among others. The study of these formations is highly convenient, as the biostratigraphic and taxonomic information obtained from them allow inferring the evolutionary pattern followed by the Pseudotissotiidae family during the early Turonian in the Iberian Trough.

2. Historical background

From the beginning of the 20th century, many ammonites have been collected from the upper Cenomanian and lower Turonian, not only in the Iberian Trough but also in the whole of Spain, and assigned to Pseudotissotiidae Hyatt, 1903, by several authors. However, only a few detailed taxonomic studies of them have ever been carried out, since only a few specimens have been described and illustrated appropriately.

Among the first systematic analysis concerning the palaeontology of the upper Cenomanian and lower Turonian cephalopods in the north of Spain, that of Karrenberg (1935) is the most noteworthy. He described many new species and mentioned several ammonite taxa, some of which can be attributed to this family. Some years later, Bataller (1950) published a synopsis on new species from the Cretaceous of Spain in which many ammonite taxa were mentioned and, among them, one pseudotissotiid.

After collecting and studying a large number of cephalopods from the Upper Cretaceous of the Iberian Trough, Wiedmann (1960, 1964) identified numerous ammonite species. He described several new taxa from the Celtiberic and Vascogotic Ranges, regions coinciding with the Central Sector and with the North-Castilian Sector and the Outer Navarro-Cantabrian

Platform, respectively. Among the obtained specimens, Wiedmann cited an important number of representatives of the family. Later, Wiedmann (1975a) described some cephalopods from the La Demanda Area, citing some members of Pseudotissotiidae. In this same year, from the ammonite sequences obtained in the Upper Cretaceous of the Central Sector, Wiedmann (1975b) obtained several pseudotissotiids and proposed some new taxa. In the Outer Navarro-Cantabrian Platform, the North Castilian Sector and the La Demanda Area, Wiedmann and Kauffman (1978) and Wiedmann (1979) identified a large number of ammonites attributed to the family.

Carretero-Moreno (1982) carried out a palaeontological investigation with specimens belonging to various groups of Cretaceous fossils, which were collected in several outcrops of the Levantine Platform and the Guadarrama Area. Cephalopods were included among the invertebrates studied in her work, some of which were pseudotissotiids. Segura and Wiedmann (1982) collected some Pseudotissotiidae in Upper Cretaceous outcrops of the Central Sector. Based on a detailed analysis of the ammonites obtained in the Guadarrama Area, Meléndez-Hevia (1984) identified a significant number of species, several of them belonging to the family Pseudotissotiidae. Studying the Turonian biostratigraphy of the Outer Navarro-Cantabrian Platform, Lamolda et al. (1989) reported some pseudotissotiids. Floquet (1991) presented a doctoral thesis in which he analysed the Upper Cretaceous geology of the northern half of the Iberian Trough and of the Basque Basin, in the north of Spain, and cited a significant number of cephalopods, including some members of Pseudotissotiidae, although he did not give any figures of them.

Santamaría-Zabala (1991, 1992, 1995) investigated the upper Cenomanian to Santonian ammonites from the North-Castilian Sector and the Outer Navarro-Cantabrian Platform, and identified several Turonian pseudotissotiids. Segura et al. (1993) studied the stratigraphic sequences deposited during the transgression of the Cenomanian-Turonian transition in some parts of the Central Sector located in the Iberian Ranges. They described some biostratigraphic sections, where members of Pseudotissotiidae were mentioned. Taking into account the ammonites studied by Santamaría-Zabala and additional information based on inoceramids, planktonic foraminifera and calcareous nannofossils, Martínez et al. (1996) cited the cephalopod taxa collected from each biozone of the upper Cenomanian to Santonian of the North-Castilian Sector, the Outer Navarro-Cantabrian Platform and the Basque Basin, among them several species of the family.

Lamolda et al. (1997) analyzed the fossils and chronostratigraphy of the Cenomanian-Turonian boundary in the Outer Navarro-Cantabrian Platform, where they found some pseudotissotiids. In the relatively deep-sea originating series of the Outer Navarro-Cantabrian Platform, Kü chler (1998) recognized some ammonites attributed to Pseudotissotiidae and presented several biostratigraphic sequences.

Recently, Barroso-Barcenilla (2004) studied the cephalopod sequence from the upper Cenomanian and lower Turonian in the northern margin of the North-Castilian Sector; and mentioned several members of Pseudotissotiidae in the presented biostratigraphic section. The conclusions reached in this work were contrasted with the ones obtained in other regions of the Iberian Trough by Barroso-Barcenilla, Goy and Segura (manuscript in review), who presented a new ammonite zonation of the upper Cenomanian and lower Turonian in the Iberian Trough, and identified several species assigned to the Pseudotissotiidae.

Likewise, in the latest years, several biostratigraphic investigations were carried out in other palaeogeographical regions adjoining to the Iberian Trough, and closely related to it, in which Upper Cretaceous cephalopod sequences were identified. Among these works, those by Wiese (1995, 1996, 1997), Wilmsen (1996, 1997a, 1997b, 2000), Wilmsen and Wiese (1996) and Wiese and Wilmsen (1999) in the North-Cantabrian Basin, and by Martínez (1982) in the Pyrenean Basin, both located in the north of Spain, should be noted.

3. Revision of pseudotissotiids of the Iberian Trough held in the collections of the GPI and the UCM

At the present time, the Wiedmann (JW), Goy (AG), Carretero (CM) and Meléndez (MH) collections of the GPI and the UCM together contain the largest number of pseudotissotiids so far collected from the upper Cenomanian and lower Turonian of the Iberian Trough. However, it has not been possible to find specimens of all the ammonite taxa cited in the works of Wiedmann (1960, 1964, 1975a, 1975b, 1979), Wiedmann and Kauffman (1978) and Segura and Wiedmann (1982) in the GPI. The investigation presented in the present work is, therefore, based exclusively on specimens that are now maintained in the JW Collection, which is why not all the taxa mentioned in the publications of Wiedmann have been revised. Likewise, it is important to emphasize that deficiencies in the method, by which the fossils of the CM Collection have been numbered and identified, have hindered adequately tracking of its ammonites. Therefore, the revision of the taxa cited by Carretero-Moreno (1982) has only been partially carried out, and, as a result, the references to this work in the synonymy of the systematic section are incomplete.

In the present paper, the palaeogeographical division (Fig. 2) and the ammonite zonation (Fig. 3) for the upper Cenomanian and lower Turonian of the Iberian Trough proposed by Barroso-Barcenilla, Goy and Segura (manuscript in review) have been followed. These authors defined several biostratigraphic units, and correlated them with ones previously recognized in the same region by other investigators and with the standard zones.

Concerning the numeration of Wiedmann's biostratigraphic units mentioned in the present article, a modification was made between the first and the latter works of this author. Wiedmann (1960, 1964) considered that the Cenomanian-Turonian boundary was located between the *Metoicoceras muelleri* and the *Metoicoceras swallowi* zones. Therefore, the latter was considered as the first biostratigraphic unit of the Turonian. The location of the boundary was later modified by Wiedmann and Kauffman (1978) and Wiedmann (1979). They held the opinion that the base of the Turonian coincided with the first occurrence of the genus *Vascoceras* Choffat, 1898. On the basis of this new premise, the *Vascoceras gamai* zone was the oldest Turonian, which is why these authors began the enumeration of their

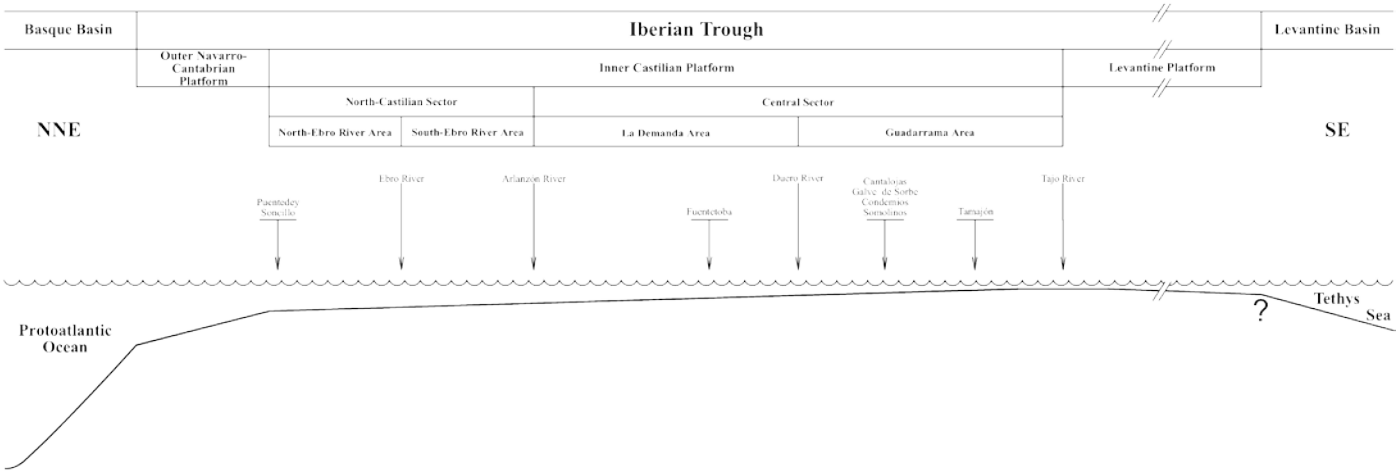

Fig. 2. Divisions followed in the Iberian Trough, the approximate locations of the outcrops studied and the geographic boundaries between their different palaeogeographic areas.
Fig. 2. Divisions du Bassin Ibérique, localisation approximative des affleurements étudiés et limites géographiques entre les différentes aires paléogéographiques.

biostratigraphic divisions from this unit. In order to avoid possible confusions, all references made in this paper to Wiedmann's biostratigraphic zones allude to his most recent works.

3.1. Thomasites *Pervinquière, 1907*

At present none of the revised collections contains specimens attributed to the type species of this genus, although Wiedmann (1960, 1964) cited *T.* cf. *rollandi* (Peron, 1889). The JW Collection keeps two ammonites assigned to the species *T.* cf. *koulabicus* (Kler, 1908) by Wiedmann (1960, 1964) that come from the zone T II of this German author in the Guadarrama Area. Although they are slightly eroded marly moulds, both show a marked ornamentation, consisting of ribs and tubercles, and a round subtriangular section. Three characteristic rows of tubercles seem to be distinguishable in their ventral regions, which remind these specimens of Kler's species. The same collection also contains some ammonites assigned by Wiedmann (1960, 1964) to *T. meslei* Pervinquière, 1907, collected from the zone T Vof the North-Castilian Sector and the La Demanda Area.

Substage	Standard ammonite zonation. Based on Kennedy (1984), Tröger & Kennedy (1996), Bengston (1996) and Gradstein et al. (2004).	North of Spain. Wiedmann & Kauffman (1978) and Wiedmann (1979).		Iberian Trough, Spain. Barroso-Barcenilla, Goy & Segura (manuscript in review). Zones	Subzones
Lower Turonian	*Mammites nodosoides*	*Wrightoceras munieri* + *Spathitoides sulcatus*	T V	*Mammites nodosoides*	*Wrightoceras munieri*
		Ingridella malladae + *Schindewolfites* spp.	T IV		*Mammites nodosoides*
	Watinoceras devonense			*Spathites (Ingridella) malladae*	*Choffaticeras (Leoniceras) luciae*
					Spathites (Ingridella) malladae
		Leoniceras discoidale + *Paramammites? saenzi*	T III	*Choffaticeras (Choffaticeras) quaasi*	
Upper Cenomanian	*Neocardioceras juddii*	*Fallotites subconciliatus*	T II	*Spathites (Jeanrogericeras) subconciliatus*	
	Metoicoceras geslinianum	*Vascoceras gamai*	T I	*Metoicoceras geslinianum*	*Vascoceras gamai*
		Metoicoceras geslinianum	C VII		*Metoicoceras geslinianum*
	Calycoceras (Proeucalycoceras) guerangeri	*Metoicoceras muelleri*	C VI	*Neolobites vibrayeanus*	*Metoicoceras mosbyense*
		Calycoceras (Lotzeites) lotzei + *Neolobites vibrayeanus*	C V		*Neolobites vibrayeanus*
		Eucalycoceras	C	*Eucalycoceras rowei*	*Calycoceras (Calycoceras) naviculare*
		spathi	IV		*Eucalycoceras rowei*

Fig. 3. Possible correlation of the biostratigraphic zonation followed in this paper and other Spanish and the standard scales.
Fig. 3. Corrélations possibles entre l'échelle biostratigraphique proposée dans ce papier et d'autres zonations espagnoles ainsi que la zonation standard.

3.2. Pseudotissotia *Peron, 1897*

The CM Collection keeps several ammonites considered by Carretero-Moreno (1982) as belonging to the type species of the genus, *P. galliennei* (d'Orbigny, 1850), obtained from the lower Turonian of the Guadarrama Area. After having examined these specimens that vary from evolute to involute moderately compressed forms, it has been stated that most of them present morphological features that seem to correspond more to some broad members of the subgenus *Choffaticeras (Choffaticeras)* Hyatt, 1903, like *C. (C.) douvillei* (Peron, 1896) and *C. (C.) segne* (Solger, 1903). However, due to their poor state of preservation, it has not been possible to carry out a precise taxonomic evaluation of these ammonites. The same collection also contains a juvenile specimen from the lower Turonian of the Guadarrama Area classified as *P. (Bauchioceras)* cf. *nigeriensis* (Woods, 1911), which is probably also attributable to the genus *Choffaticeras*.

3.3. Choffaticeras (Choffaticeras) *Hyatt, 1903*

The JW Collection has two non-illustrated specimens assigned to *C. (C.)* cf. *meslei* (Peron, 1897) obtained from undetermined lower Turonian levels of the North-Ebro Area. Although they show wider whorls and a broader umbilici than

the lectotype of Peron's species, their dimensions are similar to the ones of the more evolute and depressed specimens of *C. (C.) meslei* presented by Chancellor et al. (1994). Therefore, their morphology can be considered as being included within the broad morphological variability presented by this species. The AG and CM collections contain specimens of *C. (C.) quaasi* (Peron, 1904) coming from the eponymous zone of the Guadarrama Area. Furthermore, although Wiedmann and Kauffman (1978) and Wiedmann (1979) mentioned this species in the zone T II of the North-Castilian Sector, no specimen attributed to *C. (C.) quaasi* has been found in the JW Collection. This collection, however, contains many ammonites collected from the zone T III of the Outer Navarro-Cantabrian Platform and the Inner Castilian Platform that have been assigned by Wiedmann (1960, 1964, 1979) and Wiedmann and Kauffman (1978) to *C. (Leoniceras) discoidale* (Pervinquière, 1907), which is considered the index species of this biostratigraphic unit. Many specimens of *C. (C.) segne* (Solger, 1903) and *C. (C.)* cf. *segne* can be found in the JW Collection. They are mainly from the T III and T IV zones of the South-Ebro Area and the Central Sector. The CM Collection also keeps some members of Solger's species collected from the lower Turonian of the Guadarrama Area. The AG and MH collections have specimens of *C. (C.) pavillieri* (Pervinquière, 1907) obtained in the stratigraphically upper part of the *Choffaticeras (Choffaticeras) quaasi* zone of the Guadarrama Area. Moreover, the JW Collection contains some specimens that were attributed to *C. (C.) pavillieri* and *C. (C.)* cf. *pavillieri* by Wiedmann (1960, 1964, 1979), collected by him from his zone T IVof the South-Ebro and La Demanda areas. The AG and MH collections contain specimens of *C. (C.) sinaiticum* (Douvillé, 1928) from the *Spathites (Ingridella) malladae* subzone of the La Demanda Area. In the JW Collection some members of *C. (C.) douvillei* (Peron, 1896) and *C. (C.)* cf. *douvillei* can be found, which were obtained in the zone T IV of the North-Castilian Sector and the La Demanda Area. Likewise, the same collection keeps specimens of *Vascoceras* cf. *triangulare* Faraud, 1940, and *V. triangulare*, which was considered a synonym of *C. (C.) douvillei* by Kennedy (1994), located in the same biostratigraphical zone of the South-Ebro Area. Their morphological resemblance as well as their coinciding distributions supports the idea that *V. triangulare* could be a conspecific form of *C. (C.) douvillei*.

3.4. Choffaticeras (Leoniceras) *Douvillé, 1912*

The AG and MH collections contain specimens of the type species of this subgenus, *C. (L.) luciae* (Pervinquière, 1907), from the eponymous subzone of the Guadarrama Area, whereas *C. (L.)* cf. *luciae* is represented in the JW Collection by specimens collected from the zone T IVof the South-Ebro Area. Many members of *C. (L.) barjonai* (Choffat, 1898) are kept in the JW, AG and MH collections, obtained in the La Demanda and Guadarrama areas. Wiedmann (1960, 1964, 1975b) assigned his ammonites to the zone T IV, and the specimens kept in the UCM come from the *Choffaticeras (Leoniceras) luciae* subzone. The JW Collection also contains a doubtful ammonite assigned to *C. (L.)* cf. *barjonai* that was collected from levels attributed by Wiedmann and Kauffman (1978) and Wiedmann (1979) to the zone T II in the explanations of the plates, and to an interval comprising the T III, T IV and, with doubts, T V zones in the text. Therefore, its corresponding stratigraphic level could not be exactly determined. The same collection has specimens of *C. (L.) massipiana* (Pervinquière, 1907) and *C. (L.)* cf. *massipiana* collected by Wiedmann (1960, 1964, 1975b) from the zone T IV of the Central Sector. Some ammonites attributed to *C. (L.) philippii* (Solger, 1904) and *C. (L.)* cf. *philippii* by Wiedmann (1960, 1964, 1975b) are also kept in the JW Collection, whose temporal and geographical distributions are similar to that of the last cited taxa of Pervinquière.

3.5. Wrightoceras *Reyment, 1954*

The JW Collection has a specimen classified as *W. llarenai* (Karrenberg, 1935) that, as Wiedmann (1960, 1964) and Wiedmann and Kauffman (1978) indicated, was collected from levels assigned by them to the zone T IV of the North-Ebro Area. This collection also includes a non-illustrated ammonite from the zone T V of the South-Ebro Area and assigned to the species *W. wallsi* (Reyment, 1954). The same collection has several specimens of *W. munieri* (Pervinquière, 1907) and *W.* cf. *munieri* collected from the zone T V of the La Demanda Area, which is why Wiedmann (1960, 1964) named the biostratigraphic unit where they were found after this species. Additionally, the MH Collection contains two specimens of *W. munieri*, that were not cited by Meléndez-Hevia (1984), obtained from undetermined lower Turonian levels of the La Demanda Area. Likewise, the CM Collection has a specimen of this species from the lower Turonian of the Guadarrama Area. The JW Collection keeps two specimens from the zone T IVof the South-Ebro Area attributed to *W. mirabile* (Pervinquière, 1907) by Wiedmann (1960, 1964, 1979), and another ammonite collected from the same biostratigraphic unit of the La Demanda Area assigned to *W.* cf. *mirabile* by the same author. Although the specific identification of these three specimens seems correct, the generic one might be inaccurate. The species *W. mirabilis* was originally included in the genus *Hoplitoides* von Koenen, 1898, by Pervinquière. Several subsequent authors, however, preferred to place it in *Wrightoceras*, on the basis of the tabulate form of its venter. Nevertheless, since lately it is a commonly accepted fact that the suture line of *H. mirabilis* is closer to the family Coilopoceratidae Hyatt, 1903, than to Pseudotissotiidae Hyatt, 1903, as pointed out by Chancellor et al. (1994), and for this reason this species was assigned to *Hoplitoides* again. In our opinion, this taxonomical decision seems correct, as is justified below in the discussion of *W. munieri*. Finally, the species *W. submunieri* Wiedmann, 1975b, is represented in the JW Collection by some specimens obtained in the middle Turonian zone T IVof the Central Sector.

3.6. Donenriquoceras *Wiedmann, 1960*

The JW Collection contains specimens of *D. forbesiceratiforme* Wiedmann, 1960, probably collected from the zone

T IV of the North-Ebro Area, whereas the MH Collection also preserves members of this species from the *Wrightoceras munieri* subzone of the Guadarrama Area.

4. New data for Pseudotissotiidae in the Iberian Trough

In this section we present a systematic description of the new records of the family Pseudotissotiidae Hyatt, 1903, from the Iberian Trough, obtained during fieldwork carried out by the first author. We also describe previously unpublished members of the group identified in the AG and MH collections.

4.1. Acronyms and abbreviations

To make clear certain taxonomic comments or to indicate the location of several type specimens, the following abbreviations are used throughout the text: GPI, Institut und Museum für Geologie und Paläontologie, Tübingen, Germany; MNHN, Musée National d'Histoire Naturelle, Paris, France; SGP, Serviços Geológicos de Portugal, Lisboa, Portugal; SP, Université Sorbonne, Paris, France; UCM, Universidad Complutense de Madrid, Madrid, Spain; UPMC, Université Pierre- et-Marie-Curie, Paris, France.

4.2. Terminology

The terminology used to describe the different specimens studied is based on a glossary of morphological terms applicable to post-Triassic nautiloids and ammonoids. The glossary has been recently completed by the first author and will be published shortly.

4.3. Dimensions and location of specimens

Measurements were made with an adjustable caliper, and are given in tenths of millimetre and as percentages of the diameter of the shell. The dimensions used in the analysis are defined as follows: diameter of the shell (*D*), maximum distance between two diametrically opposite ventral extremes, measured perpendicularly to the coiling axis; whorl height (*H*), maximum distance between the ventral extreme and the most distanced point of the dorsal wall, taken parallelly to the plane of bilateral symmetry; whorl breadth (*B*), maximum distance between both flanks, measured perpendicularly to the coiling axis (tubercles and ribs have not been taken into account); umbilical width (*U*), maximum distance, taken perpendicularly to the coiling axis, separating two diametrically opposite umbilical margins of the same whorl.

All the specimens presented here are held in the Departamento de Paleontología of the UCM.

4.4. Systematic palaeontology

PSEUDOTISSOTIIDAE Hyatt, 1903

Diagnosis: Involute shells with feeble ornamentation. During ontogeny the ventrolateral and siphonal tubercles tend to merge giving rise to marked keels.

Discussion: As commented in detail below, the taxonomical status and assignation of the group has changed notably. Currently, it is generally accepted that it includes the subfamilies Pseudotissottinae Hyatt, 1903, and Hourcqiinae Renz, 1982.

Occurrence: From upper Cenomanian to Coniacian.

PSEUDOTISSOTIINAE Hyatt, 1903

[Nom. transl. Wright, 1952, p. 221, ex Pseudotissotiidae Hyatt, 1903, p. 34. Hemitissotiinae Parnes, 1964, p. 13].

Diagnosis: It includes involute genera that usually show oxyconic morphologies with compressed whorls, tectiform or tabulate venters, flat or convex flanks and reduced ornamentations. They have wide and distant umbilical tubercles, although the last whorls are usually smooth. Some of the oldest forms of this group can preserve globose appearance and may have ventrolateral and siphonal tubercles turning into keels in the typical subsequent taxa. Variable suture lines with a certain tendency to simplification.

Discussion: After considering that *Hemitissotia* Peron, 1897, is taxonomically closer related to *Pseudotissotia* Peron, 1897, *Plesiotissotia* Peron, 1897, and his new genus *Choffaticeras* than to *Tissotia* Douvillé, 1890, of Tissotiidae Hyatt, 1900, Hyatt (1903) proposed the new family Pseudotissotiidae. In spite of the systematic rank suggested by its author, this group was mainly included in Tissotiidae as a primitive subfamily, with Tissotiinae and Coilopoceratinae Hyatt, 1903, during a considerable part of the 20th century. This situation was hardly modified by Wright in Moore (1957) as he opted for maintaining Tissotiinae and Pseudotissotiinae in Tissotiidae, although he regarded Coilopoceratidae as a separate family.

The first to propose a change of the taxonomic assignation of this group was Wiedmann (1960, 1964). According to him, it was more adequate to include Pseudotissotiinae within the family Vascoceratidae Douvillé, 1912, as he observed that the relationship between the first group and Tissotiidae is very limited. Shortly later, after describing *Allotissotia*, Parnes (1964) proposed the subfamily Hemitissotiinae for the group of *Hemitissotia*, *Plesiotissotia*, *Heterotissotia* Peron, 1897, and his new genus. In their relevant work, Wright and Kennedy (1981) concurred with Wiedmann (1960, 1964) in maintaining the subfamily within Vascoceratidae, as did most subsequent authors. Renz (1982) described the family Hourcqiidae for the group of very ornamented forms with coarse ribs and umbilical and ventrolateral tubercles. Chancellor (1982) stated that the genera *Hemitissotia*, *Pseudotissotia*, *Wrightoceras* Reyment, 1954, *Thomasites* Pervinquière, 1907, *Choffaticeras*, *Donenriquoceras* Wiedmann, 1960, and, with doubts, *Eotissotia* Barber, 1957, can be included in the Pseudotissotiinae. He also added that *Plesiotissotia* and *Imlayiceras* Leanza, 1967, seem to be synonyms of *Hemitissotia* and of *Wrightoceras*, respectively.

In addition, Chancellor et al. (1994) again elevated Pseudotissotiidae to family status. They indicated that this decision was the most adequate one for a group that probably arose directly from Acanthoceratidae de Grossouvre, 1894, instead of including it within Vascoceratidae. They were also of

the opinion that Hemitissotiinae and Hourcqiidae are mere synonyms of Pseudotissotiidae. Kennedy (1994) and Wright in Kaesler (1996) maintained the taxonomic rank of Pseudotissotiidae. The latter author divided this group into the subfamilies Pseudotissotiinae and Hourcqiinae, including the genera *Thomasites*, *Pseudotissotia*, *Wrightoceras*, *Eotissotia*, *Donenriquoceras*, *Choffaticeras* and *Hemitissotia* in the former.

Referring to the phylogeny of the group, Reyment (1954, 1955) stated that the members of Pseudotissotiinae, to be precise specimens belonging to *Wrightoceras*, possibly gave rise to part of the Coilopoceratidae. After studying the type species of *Pseudotissotia* and comparing it with the genus *Wrightoceras*, Kennedy et al. (1979) considered that Pseudotissotiinae and Tissotiinae are homoeomorphic groups with a tendency to develop pseudoceratitic sutures, but that the origin of the first one lies in Acanthoceratidae, whereas they suggested that the second subfamily derived from Barroisiceratinae Basse, 1947, through *Tissotioides* Reyment, 1958. However, Cobban and Hook (1980), as well as previously Reyment (1954, 1955), upheld the existence of a direct phylogenetic lineage linking Pseudotissotiidae with Coilopoceratidae. They also remarked that the great resemblance of the suture lines of *Choffaticeras* and *Hoplitoides* reveal that it is quite probable that the relationship between both families was established by means of these two genera. Moreover, Chancellor et al. (1994) suggested that the presence of ventrolateral and siphonal tubercles in *Thomasites*, probably the oldest genus of the family, seems to reveal that Pseudotissotiidae was derived from the Acanthoceratidae. This origin could justify the exclusion of the pseudotissotiids from Vascoceratidae and its development as a clearly distinct family.

Occurrence: It occurs from upper Cenomanian to Coniacian levels of numerous regions mainly belonging to the tethyan domain. In Spain, the subfamily has been obtained in the Iberian Trough from the base of the *Spathites (Jeanrogericeras) subconciliatus* zone to levels attributed to the Coniacian.

Pseudotissotia Peron, 1897

[*Bauchioceras* Reyment, 1954, p. 157, type species by original designation *Hoplitoides nigeriensis* Woods, 1911. *Furoniceras* Collignon, 1957, p. 129 (17), type species by original designation *F. trumpyi* Collignon, 1957. Probably, *Discovascoceras* Collignon, 1957, p. 123 (11), type species by original designation *D. tesselitense* Collignon, 1957].

Type species: *Ammonites galliennei* d'Orbigny, 1850, by subsequent designation of Pervinquière (1907: p. 349).

Diagnosis: Compressed group with subrectangular or tapered whorl section. Flat or slightly arched ventral region with two or three keels. The first whorls show broad, low and sparse ribs and elongated ventrolateral tubercles on outer keels. During ontogeny the ornamentation subdues and the whorl section becomes rounded, with a nearly smooth adult body chamber. The suture line has four saddles per flank with few incisions.

Discussion: The numerous morphological resemblances and the probable phylogenetic proximity between *Pseudotissotia* and *Thomasites* Pervinquière, 1907, make it difficult to assign some badly preserved specimens to either genus. However, the second group is generally characterized by wider and more depressed shells, more triangular whorl sections and more coarse ornamentations than the first group, which helps to distinguish them.

Not long after having erected, in 1957, the new genus *Discovascoceras* and its type species, *D. tesselitense*, Collignon (1965) already emphasized the notable similarity between this species and *P. adkinsi* Kummel and Decker, 1954. Later, Reyment (1978) regarded *Discovascoceras* as a subgenus of *Bauchioceras* Reyment, 1954, and indicated that the strange suture line of *Furoniceras trumpyi* Collignon, 1957, type species of *Furoniceras* Collignon, 1957, seems to have been caused by eolian erosion. Moreover, Kennedy et al. (1979) observed a great morphological resemblance between *P. galliennei* (d'Orbigny, 1850) and *Hoplitoides nigeriensis* Woods, 1911, type species of *Bauchioceras*. On this basis, the same authors stated that this group should be considered as a synonym of *Pseudotissotia* and rejected the maintenance of a generic or subgeneric division, which has been accepted by most of the subsequent authors. Kennedy et al. (1979) also remarked that the only feature separating *D. tesselitense* from *P. nigeriensis tricarinata* (Reyment, 1954) is that the first taxon is slightly more evolute. In view of this, they suggested that *Discovascoceras* might be a synonym of *Pseudotissotia*. Later, Wright in Kaesler (1996) mentioned this possibility in his work. In our opinion, *Bauchioceras*, *Furoniceras* and, probably, *Discovascoceras* should be included in the synonymy of *Pseudotissotia*.

Apart from the type, *P. nigeriensis*, *P. gabonensis* Lombard, 1930, *P. adkinsi* and the rare ?*P. inopinata* Kennedy and Bayliss, 1977, are among the species attributed to *Pseudotissotia*. The relationships between *P. galliennei* and other forms of the genus have been thoroughly analysed by Kennedy et al. (1979), who pointed out the possibility that *P. gabonensis* could be a synonym of the species of d'Orbigny. Years later, Meister et al. (2003) considered that *P. gabonensis* is a conspecific form of *P. nigeriensis*. Therefore, it should be emphasized that the different species assigned to *Pseudotissotia* are normally endowed with a wide morphological variability, although they usually tend to lose their ornamentation as they approach maturity.

In relation to the phylogeny of the group, Meister (1989) and Wright in Kaesler (1996) suggested that it could be derived from *Thomasites*. Nevertheless, some records of *Pseudotissotia* seem to be below the lowest members of *Thomasites*, a problem which has not been solved yet.

Occurrence: This genus has been identified in the lower and middle Turonian of France, Spain, North and West-Africa, Syria, Israel, the USA, Mexico, Central-America, Colombia and Brazil.

Pseudotissotia sp.

Fig. 4(1–3)

Material and dimensions:

	D	*H* (%)	*B* (%)	*U* (%)
CA-R-182	1296	574 (44)	360 (28)	284 (22)

Fig. 4. 1, 2, 3. *Pseudotissotia* sp., specimen CA-R-182, from an unknown lower Turonian level of Condemios, × 1. 1. Ventral view. 2. Lateral view. 3. Apertural view. 4, 5. *Choffaticeras (Choffaticeras) quaasi* (Peron, 1904), specimen CB-R-662, from the *Choffaticeras (Choffaticeras) quaasi* zone of Condemios, × 1. 4. Ventral view. 5. Lateral view.

Description: Medium-sized compressed ammonite with from subrectangular to subeliptical whorl section. From tabulate to tricarinate ventral region, arched flanks and umbilicus with subvertical walls. The keels disappear during growth and venter and flanks become arched. Relatively simple suture line.

Discussion: Despite the abovementioned problematical proximity between *Pseudotissotia* and *Thomasites* Pervinquière, 1907, the compressed and subrectangular section, the relatively broad umbilicus and the lack of ornamentation of this specimen are features more compatible with the ones of the Peron's group.

It also presents notable similarities with *P. nigeriensis* (Woods, 1911). As stated by Hirano (1983), Meister (1989) and Amédro et al. (1996), this species reaches a considerable morphological variability, ranging from compressed and smooth with marked keels to relatively depressed and ornamented specimens. A consequence of this morphological variability was the division of this species into several different subspecies, like *P. nigeriensis tricarinata* (Reyment, 1954), *P. nigeriensis macrocarinata* Barber, 1957, *P. nigeriensis plana* Barber, 1957, *P. nigeriensis bicarinata* Barber, 1957, *P. nigeriensis tabulata* Barber, 1957, and *P. nigeriensis egrediens* Collignon, 1965, and the assignation of different synonyms to the same taxon by many authors, as Hirano (1983). Although some of the forms attributable to this species, like *P. nigeriensis egrediens*, indeed show morphological features and temporal distributions coinciding with those of the specimen presented herein, none of them reaches the necessary resemblance in order to attribute CA-R-182 with certainty to it. Likewise, *P. nigeriensis* shows less rounded whorl with commonly smaller umbilicus of subvertical margin, almost flat flanks, markedly tricarinate ventral region, and habitually noticeable ribs and tubercles. On the other hand, both ?*P. inopinata* Kennedy and Bayliss, 1977, as well as *P. gabonensis* Lombard, 1930, have more ornamented shells and other features that does not coincide with the ones of the specimen here described. *D. tesselitense* presents a proportionally broader whorl section with a marked subtriangular profile.

Within other groups, *Pseudotissotia* sp. also maintains certain resemblance to *Thomasites adkinsi* (Kummel and Decker, 1954), especially with specimen PMMA 34 of Chancellor (1982: Figs. 68, 69). Nevertheless, the members of this species show more vertical umbilical walls and relatively wider whorl sections than our specimen.

Occurrence: It was collected from the base of the *Choffaticeras (Choffaticeras) quaasi* zone of Condemios, in the Guadarrama Area of the Iberian Trough, Spain, but the exact level could not exactly be determined.

Choffaticeras Hyatt, 1903

Type species: *Pseudotissotia meslei* Peron, 1897, by original designation.

Diagnosis: Involute shells with lanceolate or subtriangular sections ranging from very compressed to slightly depressed, reaching their greatest breadth close to the umbilical margins. Relatively small and deep umbilici and narrow, sharp or rounded venters with continuous siphonal keels, occasionally flanked by two keels or feeble ventrolateral tubercles. Some species have biconcave flanks forming a bell-shaped section. The first whorls may show fine ornamentation consisting of dense ribbing and weak umbilical and ventrolateral tubercles that disappear quite soon during ontogeny. The adult specimens are smooth and range from medium to large sizes. Very variable suture lines that maintain certain resemblance to that of *Pseudotissotia*, Peron, 1897, and presents deep incisions at the first lateral saddles.

Discussion: Hyatt (1903) noticed that some of the forms assigned until then to *Pseudotissotia* are more involute and compressed, despite having the typical suture lines of this group. For this reason, he described the genus *Choffaticeras*, in which he included, apart from *P. meslei*, Peron, 1897, considered the type species, *P. barjonai* Choffat, 1898, and, doubtfully, *P. douvillei* Peron, 1897. A few years later, Pervinquière (1907) included this group in *Pseudotissotia* as a subgenus. Within *P. (Choffaticeras)* he distinguished two groups characterised, respectively, by tricarinate and by monocarinate species. In the first one, he included *P. meslei*, *P. ganiveti* (Coquand, 1859), *P. segnis* Solger, 1903 and *P. pavillieri* Pervinquière, 1907, and in the second one *P. barjonai*, *P. philippii* Solger, 1904, *P. luciae* Pervinquière, 1907, *P. massipiana* Pervinquière, 1907, and, although uncertain, *P. douvillei*. After observing that the lateral lobe of *P. meslei* is symmetrical, whereas *P. segnis*, *P. pavillieri*, *P. luciae* and *P. douvillei* present an asymmetrical one, Douvillé (1912) proposed the new genus *Leoniceras* for group these taxa. Years later, Reyment (1955) redefined the genus on the basis of the observations of Pervinquière, dividing the group into the tricarinate, *C. (Choffaticeras)*, and the monocarinate, *C. (Leoniceras)*, forms. This systematic proposal, with which we agree, was already accepted by Wright in Moore (1957) and subsequently by Kennedy (1994), Chancellor et al. (1994) and Wright in Kaesler (1996), among others.

The limits between the numerous species assigned to the genus *Choffaticeras* are hard to set, as among many of them a constant morphological variability can be observed. For example, after thoroughly analysing the differences that allow some forms of the group to be distinguished, Freund and Raab (1969) noticed intermediate morphologies between *C. (C.) segne*, *C. (C.) quaasi* (Peron, 1904) and *C. (C.) pavillieri*, between the first one and *C. (C.) securiforme* (Eck, 1909) and between the third one and *C. (C.) sinaiticum* (Douvillé, 1928). Among the monocarinate members of *Choffaticeras*, these authors also observed transitional forms between *C. (L.) barjonai*, with a wider whorl section and a narrower umbilicus,

Fig. 4. 1, 2, 3. *Pseudotissotia* sp., spécimen CA-R-182, d'un niveau Turonien inférieur inconnu de Condemios, × 1. 1. Vue ventrale. 2. Vue latérale. 3. Vue aperturale. 4, 5. *Choffaticeras (Choffaticeras) quaasi* (Peron, 1904), spécimen CB-R-662, de la zone à *Choffaticeras (Choffaticeras) quaasi* de Condemios, × 1. 4. Vue ventrale. 5. Vue latérale.

and *C. (L.) luciae*, with a narrower section and a greater umbilical width.

Although many taxa have been attributed to *Choffaticeras* in the past, after studying their features and records and contrasting them with the new information obtained recently, the following species can be identified in the genus.

C. (C.) meslei must be highlighted among the tricarinate species of *Choffaticeras*. It shows the diagnostic features of the genus and a ventral region resembling *Pseudotissotia*, from which *Choffaticeras* seems to derive. A continuous series consisting of the species *C. (C.) segne*, *C. (C.) quaasi* and *C. (C.) pavillieri* can be defined. In it, the dimensions of the whorl breadth and the umbilical width decrease in a constant manner. Furthermore, *C. (C.) douvillei* presents a wide and subtriangular whorl section and a relatively narrow umbilicus, similar to *C. (C.) meslei*, whereas *C. (C.) securiforme* shows well differentiated and defined morphological features. *C. (C.) sinaiticum*, which exhibits a very compressed and involute section, apparently belonging to the tricarinate species but, in fact, it acts as a transitional form between them, exactly *C. (C.) pavillieri*, and the monocarinate members of the genus.

Among the species of *Choffaticeras* with only one keel another continuous series consisting of *C. (L.) luciae* and *C. (L.) barjonai* can be identified, in which the proportions of the umbilical width and the whorl breadth widen in a continuous manner. *C. (L.) massipiana* is characterized by a very narrow whorl section and a quite broad umbilicus, and *C. (L.) philippii* has conspicuous ribbing and a form that resembles that of *C. (L.) luciae*.

It cannot be denied that some of these taxa, especially those included in the continuous series, may in fact be conspecific, but for the moment we have opted for maintaining them separate. It seems that almost all of the remaining forms attributed to this genus, like *Pseudotissotia (Choffaticeras) segnis* Solger var. *discoidalis* Pervinquière, 1907, *Pseudotissotia (Choffaticeras) luciae* var. *stricta* Pervinquière, 1907, *Tissotia schweinfurthi* Eck, 1909, *Pseudotissotia (Choffaticeras) mokattanica* Greco, 1915, *Pseudotissotia (Choffaticeras) destefanii* Greco, 1915, *Leoniceras carinifer* Douvillé, 1928, *Leoniceras kenehense* Douvillé, 1928, *Pseudotissotia (Leoniceras) alaouitense* Basse, 1937, *Leoniceras luciaeformis* Faraud, 1951, and *Choffaticeras luciae trisellatum* Freund and Raab, 1969, could be included within the range of variation of the previously cited species.

Phylogenetically, as has been pointed out above, the genus *Choffaticeras* seems to derive from *Pseudotissotia* by elevation of the keel. According to Freund and Raab (1969: p. 54), *C. (C.) meslei* is the oldest species of this group. Its wide whorl section and its tricarinate and rounded ventral region are similar to the typical ones of *Bauchioceras* Reyment, 1954, that has subsequently been considered a synonym of *Pseudotissotia*. Likewise, some authors stated certain phylogenetical resemblance between *Choffaticeras* and the Coniacian genus *Hemitissotia* Peron, 1897.

Occurrence: Its species have been identified in the lower and middle Turonian of France, Spain, Portugal, Algeria, Tunisia, Nigeria, Cameroon, Madagascar, Egypt, Syria, Jordan, Israel and the USA, and is thus a typical group of the Tethys Sea. The genus has been found in the Iberian Trough from the *Choffaticeras (Choffaticeras) quaasi* zone to the *Choffaticeras (Leoniceras) luciae* subzone.

Choffaticeras (Choffaticeras) Hyatt, 1903

Type species: *Pseudotissotia meslei* Peron, 1897, by original designation.

Diagnosis: It presents two ventrolateral keels that on the first whorls can be substituted by the same number of rows of rounded or slightly elongated tubercles.

Discussion: After the description of Douvillé (1912) of the genus *Leoniceras*, the tricarinate species were considered as the only members of *Choffaticeras* by Basse (1952), and as a subgenus of *Pseudotissotia* by Roman (1938), amongst others. Nevertheless, the tricarinate species were grouped some years later in the subgenus *C. (Choffaticeras)* by Reyment (1955). This taxonomic procedure was followed by Wright in Moore (1957) and by many other subsequent authors.

Occurrence: Both the temporal and geographical distributions are similar to the genus.

Choffaticeras (Choffaticeras) quaasi (Peron, 1904)

Figs. 4(4, 5) and 5(1)

1904. *Schloenbachia quaasi* – Peron, p. 255, Pl. 1, Figs. 1–3.

1907. *Pseudotissotia (Choffaticeras) segnis* Solger var. *discoidalis* – Pervinquière, p. 352, Pl. 23, Fig. 3a, b.

non 1914. *Pseudotissotia segnis* Solger var. *discoidalis* Pervinquière – Eck, p. 207, Pl. 14, Fig. 7; Pl. 15, Fig. 1; Text-Figs.7–9 (? = *C. (C.) pavillieri*).

1914. *Schloenbachia quaasi* Fourtau – Eck, p. 212, Pl. 13, Figs. 3–7; Pl. 14, Figs. 2–5, 7.

1915. *Schloenbachia quaasi* Peron – Greco, p. 209, Pl. 17, Fig. 6.

1915. *Pseudotissotia (Choffaticeras) segnis* Solger var. *discoidalis* Pervinquière – Greco, p. 214, Pl. 19, Fig. 4 [non Pl. 19, Figs. 2, 3 (? = *C. (C.) sinaiticum*)].

1920. *Pseudotissotia segnis* var. indet. – Taubenhaus, p. 42, Pl. 4, Figs. 1a, b, 2.

?1920. *Pseudotissotia macrodiscus* Schweinfurth – Taubenhaus, p. 42, Pl. 4, Fig. 4a, b.

1928. *Leoniceras quaasi* (Peron) – Douvillé, p. 21, Pl. 3, Figs. 2, 3, 6, 7 [non Pl. 3, Figs. 4, 5; Pl. 4, Figs. 1, 2 (= *C. (C.) pavillieri*)].

1940. *Leoniceras segne* (Solger) var. *discoidalis* (Pervinquière) - Fabre, p. 297, Fig. 51.

1951. *Leoniceras quaasi* (Peron) – Faraud, p. 154.

1951. *Leoniceras segne* (Solger) – Faraud, p. 155, Text-Fig. 2.

1960. *Choffaticeras (Leoniceras) discoidale* (Pervinquière) – Wiedmann, pp. 712, 716, 720.

1964. *Choffaticeras (Leoniceras) discoidale* (Pervinquière) – Wiedmann, pp. 111–112, 115.

1969. *Choffaticeras quaasi* (Peron) – Freund and Raab, p. 56, Pl. 9, Figs. 5, 6; Text-Figs. 10m, 11a.

1978. *Choffaticeras quaasi* (Peron) – Wiedmann and Kauffman, Pl. 9, Fig. 2.

1978. *Leoniceras discoidale* (Pervinquière) – Wiedmann and Kauffman, pp. 3–4.

Fig. 5. 1. *Choffaticeras (Choffaticeras) quaasi* (Peron, 1904), specimen CB-R-662, from the *Choffaticeras (Choffaticeras) quaasi* zone of Condemios, lateral view, × 1. 2, 3, 4. *Choffaticeras (Choffaticeras) pavillieri* (Pervinquière, 1907), specimen PU-S-240, from the *Spathites (Ingridella) malladae* zone of Puentedey, × 1. 2. Ventral view. 3. Apertural view. 4. Lateral view. 5. *Choffaticeras (Choffaticeras) segne* (Solger, 1903), specimen MS-5, ventral view, × 1.

Fig. 5. 1. *Choffaticeras (Choffaticeras) quaasi* (Peron, 1904), spécimen CB-R-662, de la zone à *Choffaticeras (Choffaticeras) quaasi* de Condemios, vue latérale, × 1. 2, 3, 4. *Choffaticeras (Choffaticeras) pavillieri* (Pervinquière, 1907), spécimen PU-S-240, de la zone à *Spathites (Ingridella) malladae* de Puentedey, × 1. 2. Vue ventrale. 3. Vue aperturale. 4. Vue latérale. 5. *Choffaticeras (Choffaticeras) segne* (Solger, 1903), spécimen MS-5, vue ventrale, × 1.

1979. *Choffaticeras quaasi* (Peron) – Wiedmann, Pl. 9, Fig. 2.

1979. *Leoniceras discoidale* (Pervinquière) – Wiedmann, p. 176.

1982. *Choffaticeras discoidale* (Pervinquière) – Segura and Wiedmann, p. 296, Pl. 1, Figs. 1, 2.

1982. *Leoniceras quaasi* (Peron) – Carretero-Moreno, p. 269.

1984. *Choffaticeras quaasi* (Peron) – Meléndez-Hevia, p. 107, Pl. 12, Fig. 3 [only].

?1989. *Choffaticeras* gr. *quaasi* (Peron) – Meister, p. 58, Pl. 27, Fig. 4.

1991. *Choffaticeras quaasi* (Peron) – Santamaría-Zabala, p. 156, Pl. 10, Fig. 4.

1994. *Choffaticeras (Choffaticeras) quaasi* (Peron) – Chancellor et al., p. 88, Pl. 28, Figs. 5–7.

1995. *Choffaticeras quaasi* (Peron) – Santamaría-Zabala, p. 52, Pl. 2, Fig. 1.

1998. *Choffaticeras quaasi* (Peron) – Küchler, Pl. 9, Fig. 8.

? aff. 2005. *Choffaticeras* aff. *quaasi* (Peron) – Meister and Abdallah, p. 138, Pl. 19, Fig. 1; Text-Fig. 26.

Type: Without designation

Material and dimensions:

	D	*H* (%)	*B* (%)	*U* (%)
CB-R-662	775	410 (53)	243 (31)	89 (11)
PU-S-351	rv860	rv440 (51)		rv85 (10)
PU-S-355	rv650	rv340 (52)	rv242 (37)	rv62 (10)
PU-S-443	376	187 (50)	119 (32)	54 (14)
TA-S-55	rv1150	rv570 (50)	rv243 (21)	rv154 (13)
TA-S-56	1134	550 (49)	270 (24)	129 (11)

Description: Specimens with very involute whorls, oval compressed sections and slightly arched or flat flanks. Very small and deep umbilici with vertical walls and rounded margins. Narrow tectiform sharp or rounded venters each bearing a higher siphonal and two lower ventrolateral keels that disappear before the adult body chamber is reached. These ammonites lack ornamentation or it is reduced to feeble prorsiradiate plications, alternating long with short ones. They are situated on the flanks and may coarsen slightly as they reach the umbilical and ventrolateral margins, on which there can arise small tubercles. The suture lines are typical of the genus, with pseudoceratitic appearance and bifid or trifid wide and asymmetrical lateral lobes. Due to the post mortem deformation the whorl sections might narrow, which is why the flanks of some specimens become slightly concave near the ventrolateral margin.

Discussion: The typical features of some forms of the subgenus allow us to distinguish them very easily from *C. (C.) quaasi*. The whorl section of *C. (C.) sinaiticum* (Douvillé, 1928) rapidly sharpens with growth, contrary to the group's remaining species. *C. (C.) meslei* has a wider whorl and maintains a marked tricarinate venter during ontogeny. *C. (C.) douvillei* also presents a notably more depressed shell. The ventral region of *C. (C.) securiforme* evolves on a very typical form, giving rise to a rare groove on the ventrolateral region, which differentiates this species from *C. (C.) quaasi*. Likewise, the rounded venter developed by some adult specimens of *C. (C.) quaasi* makes it relatively easy to identify them.

Nevertheless, sometimes it is considerably hard to distinguish this species from other taxa of the subgenus. As Freund and Raab (1969) already remarked and has also been detailed above in the discussion of this genus, the main difficulty lies in distinguishing *C. (C.) quaasi* from *C. (C.) segne* and, especially, from *C. (C.) pavillieri*. The limits between these three species are arbitrary as the morphological features vary constantly. For these authors *C. (C.) segne* would include those specimens with a more depressed whorl section whose breadth exceeds two thirds of its height, and have a relatively broad umbilicus. Slightly more compressed specimens with a bit narrower umbilicus whose width is not wider than two thirds of the whorl breadth would be included within *C. (C.) quaasi*. The most depressed forms of *C. (C.) quaasi* and, therefore, with intermediate dimensions between this species and *C. (C.) segne* would correspond to *Pseudotissotia (C.) segnis* Solger var. *discoidalis* Pervinquière, 1907, which can be considered a mere synonym of the Peron's species. Finally, the most compressed specimens with the narrowest umbilicus would be grouped in *C. (C.) pavillieri*. Likewise, Freund and Raab (1969) also described transitional forms between the latter species and the rare *C. (C.) sinaiticum* Douvillé, 1928. Although this species shows a tricarinate juvenile morphology, it loses the lateral keels during the first ontogenetic stages, and soon develops a very compressed discoidal shell with a relatively sharp ventral region. Therefore, broadly speaking, *C. (C.) segne* has a slightly wider section and a broader umbilicus, and *C. (C.) pavillieri* presents a more compressed shell with smaller umbilical width, maintaining until the adult body chamber a sharper siphonal keel than *C. (C.) quaasi*.

Although the proportions of the whorl and the umbilical width are the main features that allow differentiating *C. (C.) quaasi* from *C. (C.) pavillieri*, it should be noted that post mortem deformation might alter these dimensions, affecting the compression of the shell. Therefore, for identifying these two taxa more precisely it is useful to regard other parameters that are more evident in one of the two species. Both *C. (C.) quaasi* as well as *C. (C.) pavillieri* show ribs during the first ontogenetic stages, but the ones of the former species reach a greater breadth and are separated by wider intercostal spaces, reaching a lower number per whorl. The keels of *C. (C.) quaasi* disappear earlier than those of *C. (C.) pavillieri*, that maintains the siphonal keel on the adult body chamber. The umbilical margin of *C. (C.) quaasi* seems to be narrower and, therefore, more abrupt than that of *C. (C.) pavillieri*. The suture line of *C. (C.) quaasi* is slightly more simple than that of *C. (C.) pavillieri*. It has also been stated that most specimens of *C. (C.) quaasi* have a lower whorl expansion rate than *C. (C.) pavillieri*. Finally, it has been noticed that, in Spain, the first records of *C. (C.) quaasi* are older than the ones assigned to *C. (C.) pavillieri*, which coincides, amongst others, with the observations made in Israel by Freund and Raab (1969). In relation to the whorl section of *C. (C.) quaasi*, Chancellor et al. (1994) pointed out that its greatest breadth is located near the umbilical

margin whereas, Santamaría-Zabala (1991, 1995) indicated that it is situated in the middle part of the flanks of the specimens examined by him. This feature can thus not be considered diagnostic, as it is very variable and can easily be altered by sedimentary deformation.

In spite of these differences, intermediate specimens occur with typical features of *C. (C.) quaasi* and *C. (C.) pavillieri* that are difficult to assign to one of these two species. Among these, can be mentioned the specimen classified as *Pseudotissotia macrodiscus* Schweinfurth (m.s.p.) by Taubenhaus (1920), which was attributed to *C. (C.) pavillieri* by Freund and Raab (1969). Although this specimen shows a tectiform ventral region with an elevated siphonal keel, it has proportions that are closer to *C. (C.) quaasi*. For this reason, concurring with Taubenhaus (1920: pp. 42–43), we have considered the taxon of Schweinfurth as a probable synonym of the Peron's species. The specific assignation of the Egyptian ammonite classified as *Pseudotissotia segnis* discoidalis by Eck (1914) and of the Algerian one attributed to *Leoniceras pavillieri* by Collignon (1957, 1965) is also considerably doubtful, as is indicated below, in the discussion of *C. (C.) pavillieri*.

P. (C.) segnis discoidalis, originally described by Pervinquière (1907) as a variety including the most compressed forms of *P. segnis* Solger, 1903, was considered a mere synonym of *C. (C.) quaasi* by Freund and Raab (1969) and many other subsequent authors, such as Santamaría-Zabala (1991, 1995) and Chancellor et al. (1994). The dimensions of the original specimen provided by Pervinquière (1907), which are 96 mm of diameter, 50 mm of whorl height, 32 mm of whorl breadth and 17 mm of umbilical width, reveal that the proportions of *P. (C.) segnis discoidalis* are not distinguishable from those attributed to *C. (C.) quaasi*. Likewise, the geographical and temporal distributions in the Iberian Trough of both these taxa can be regarded fairly coincident, due to which it seems adequate to consider both forms as conspecific. Similarly, the shape and proportions of *Pseudotissotia segnis* var. indet. Taubenhaus, 1920, coincide precisely with typical forms of *C. (C.) quaasi*.

The *Leoniceras quaasi* illustrated by Douvillé (1928: Pl. 3, Figs. 4, 5) was assigned to *C. (C.) pavillieri* by Freund and Raab (1969) and was excluded from the synonymy of Peron's species by Chancellor et al. (1994). However, due to the limited number of dimensions provided by Douvillé (1928), his specimens can unfortunately not be attributed with certainty to either species. Nevertheless, according to the proportions obtained from their respective photographs the ammonites of the Figs. 2-3 and 6-7 of the Plate 3, seem to resemble to *C. (C.) quaasi*, and the specimens of the Figs. 4-5 of the Plate 3 and the Figs. 1-2 of the Plate 4 seem close to *C. (C.) pavillieri*. The dimensions of the *Leoniceras segne* of Faraud (1951: p. 155, Text-Fig. 2), of which he only illustrated the suture line, coincide with those of the variety *discoidale* and can, therefore, be considered a specimen of *C. (C.) quaasi*. Although the *C.* gr. *quaasi* of Meister (1989) presents some typical features of Peron's species, its ventral region seems strikingly flat and broad. Finally, the *C.* aff. *quaasi* of Meister and Abdallah (2005) has an umbilical width near to 20 per cent of the diameter of the shell and a morphology close to *Pseudotissotia* Peron, 1897, but shows the typical suture line of *Choffaticeras (Choffaticeras)* Hyatt, 1903. These features make its taxonomical classification very difficult.

Occurrence: It has been cited from the lower to the middle Turonian of Egypt, Tunisia, Jordan, France, Spain, Israel and, with doubts, Nigeria. In the Iberian Trough, this species has been collected by us from the *Choffaticeras (Choffaticeras) quaasi* zone of the Inner Castilian Platform, but it was also registered in the lower Turonian of the Outer Navarro-Cantabrian Platform by other authors, such as Santamaría-Zabala (1991, 1995) and Küchler (1998). With regard to the ornamentation, it has been observed that juvenile specimens of *C. (C.) quaasi* and *C. (C.) pavillieri* collected in this region, some of which were illustrated by Wiedmann and Kauffman (1978), Wiedmann (1979) and Santamaría-Zabala (1991, 1995), are characterized by a much more subdued ribbing than the ones from other basins.

Choffaticeras (Choffaticeras) pavillieri Pervinquière, 1907
Fig. 5(2–4)

1907. *Pseudotissotia (Choffaticeras) pavillieri* – Pervinquière, p. 353, Pl. 23, Figs. 4–6; Text-Fig. 134.

1912. *Leoniceras pavillieri* (Pervinquière) – Douvillé, p. 312, Text-Fig. 50.

?1914. *Pseudotissotia segnis* Solger var. *discoidalis* Pervinquière – Eck, p. 207, Pl. 14, Fig. 7; Pl. 15, Fig. 1; Text-Figs. 7–9.

1928. *Leoniceras quaasi* (Peron) – Douvillé, p. 21, Pl. 3, Figs. 4, 5; Pl. 4, Figs. 1, 2.

1928. *Leoniceras carinifer* – Douvillé, p. 25, Pl. 4, Fig. 3a.

1931. *Pseudotissotia (Choffaticeras) pavillieri* Pervinquière – Basse, p. 40, Pl. 9, Fig. 23; Pl. 13, Fig. 2.

1939. *Pseudotissotia (Leoniceras) pavillieri* Pervinquière – Basse, p. 51, Pl. 3, Fig. 13; Text-Fig. 6a–c.

1951. *Leoniceras pavillieri* (Pervinquière) – Faraud, p. 153, Text-Fig. 4.

?1957. *Leoniceras pavillieri* (Pervinquière) – Collignon, p. 130.

1960. *Choffaticeras (Leoniceras) pavillieri* (Pervinquière) – Wiedmann, pp. 712, 720, 723.

cf. 1960. *Choffaticeras (Leoniceras)* cf. *pavillieri* (Pervinquière) – Wiedmann, p. 712.

1964. *Choffaticeras (Leoniceras) pavillieri* (Pervinquière) – Wiedmann, pp. 111, 115–116.

cf. 1964. *Choffaticeras (Leoniceras)* cf. *pavillieri* (Pervinquière) – Wiedmann, p. 111.

?1965. *Leoniceras pavillieri* (Pervinquière) – Collignon, p. 190.

1969. *Choffaticeras pavillieri* (Pervinquière) – Freund and Raab, p. 56, Pl. 9, Figs. 3, 4; Text-Fig. 11b–d.

1972. *Choffaticeras pavillieri* (Pervinquière) – Cobban and Scott, p. 92, Pl. 34, Figs. 3–6; Pl. 35, Figs. 1–3; Text-Fig. 52.

1979. *Leoniceras pavillieri* (Pervinquière) – Wiedmann, p. 193.

1984. *Choffaticeras quaasi* (Peron) – Meléndez-Hevia, Pl. 12, Fig. 4a, b [only].

cf. 1985. *Choffaticeras* cf. *pavillieri* (Pervinquière) – Amédro and Hancock, Fig. 10a, b.

1986. *Choffaticeras pavillieri* (Pervinquière) – Szász, p. 129, Pl. 2, Fig. 3; Pl. 5, Figs. 3, 4; Pl. 6, Figs. 1, 3.

?1989. *Choffaticeras* gr. *pavillieri* (Pervinquière) juv. – Meister, Pl. 27, Fig. 5.

1989. *Choffaticeras pavillieri* (Pervinquière) – Lamolda et al., Fig. 3(2).

1991. *Choffaticeras pavillieri* (Pervinquière) – Santamaría-Zabala, p. 158, Pl. 9, Fig. 6.

1992. *Choffaticeras pavillieri* (Pervinquière) – Thomel, p. 236, Pl. 128, Figs. 5, 6.

1994. *Choffaticeras (Choffaticeras) pavillieri* (Pervinquière) – Chancellor et al., Pl. 26, Figs. 6, 7, 9–12.

1995. *Choffaticeras pavillieri* (Pervinquière) – Santamaría-Zabala, p. 53, Pl. 2, Fig. 3; Text-Fig. 1c.

?1996. *Choffaticeras* gr. *pavillieri* (Pervinquière) – Meister and Abdallah, p. 15, Pl. 5, Fig. 1; Text-Fig. 6h, i.

?1996. *Choffaticeras* gr. *quaasi* (Peron)-*pavillieri* Pervinquière – Amédro et al., p. 221, Pl. 10, Fig. 1.

?1997. *Choffaticeras pavillieri* (Pervinquière) – Wiese, Pl. 1, Figs. 2, 3, 5, 6.

1997. *Choffaticeras pavillieri* (Pervinquière) – Lamolda et al., p. 349, Fig. 9e.

2005. *Choffaticeras pavillieri* (Pervinquière) – Meister and Abdallah, p. 138, Pl. 19, Fig. 2.

Type: The holotype by original designation is the specimen of Pervinquière (1907: p. 353, Pl. 23, Fig. 5a, b; Text-Fig. 134) collected from the lower Turonian of Nakhla, Tunisia.

Material and dimensions:

	D	*H* (%)	*B* (%)	*U* (%)
PU-R-358		498	246	57
PU-S-240	1355	728 (54)	285 (21)	119 (9)
PU-S-243	785	429 (55)	205 (26)	72 (9)
PU-S-296	1032	555 (54)	rv176 (17)	93 (9)
TA-S-54	785	416 (53)	182 (23)	76 (10)
TA-S-67	1066	545 (51)	268 (25)	94 (9)
TE-S-74	862	484 (56)	244 (28)	rv75 (9)

Description: Very involute discoidal specimens with compressed and fragile subogival whorl sections. The narrow venter is very typical, with a high and sharp siphonal keel maintained in all whorls and flanked by two feeble ventrolateral carinas. The flanks are slightly convex, almost flat, and their umbilici are very small and relatively shallow. During the first stages of growth about 20 broad, weak, prorsiradiate, concave and widely distant primary ribs arise per whorl, bearing weak and elongated ventrolateral tubercles. Some evenly intercalated accessory ribs may appear. The whorl becomes slightly more involute during ontogeny, the section reaches its greatest breadth close to the middle part of the flank, and the ornamentation progressively disappears, although some tubercles and ribs, only distinguishable from the umbilical margin to the inner part of the flank, can remain. The suture lines exhibit numerous elements and broad ventral lobes.

Discussion: The very compressed whorl section, the narrow umbilicus and the siphonal keel, which remains in the adult body chamber, facilitate the identification of this species. As already pointed out, *Choffaticeras (Choffaticeras) quaasi* (Peron, 1904) has a broader section, a slightly wider umbilicus, a juvenile ornamentation bearing fewer ribs per whorl and a less complex suture line, whereas *C. (Leoniceras) luciae* (Pervinquière, 1907) presents a much broader umbilicus and a subtriangular whorl section. Some specimens of the genus *Coilopoceras* Hyatt, 1903, may also resemble this species but, as noted by Freund and Raab (1969), the members of this group lack ornamentation and have broader first lateral lobes.

Freund and Raab (1969) doubtfully included *Leoniceras carinifer* Douvillé, 1928, in the synonymy of this species, although they did not give an explanation for doing so. Later, Cobban and Scott (1972) and Chancellor et al. (1994), among others, also considered *L. carinifer* as a synonym. The dimensions of the specimen provided by Douvillé (1928: p. 25) and the general appearance of it reveal that it is notably compressed, with a narrow umbilicus, whose breadth makes up nearly seven per cent of the diameter of the shell, a high whorl expansion rate and a conspicuous siphonal keel. All these features coincide wholly with those attributed to *C. (C.) pavillieri*.

Pseudotissotia segnis discoidalis of Eck (1914) and *Leoniceras pavillieri* of Collignon (1957, 1965) show intermediate features between *C. (C.) quaasi* and *C. (C.) pavillieri*. The former has a very small umbilicus and seems to be closer to *C. (C.) pavillieri*. Likewise, the latter specimen, included by Amédro et al. (1996) within their group *C. quaasi-pavillieri*, also exhibits a morphology slightly more converging with the species of Pervinquière, as was emphasized by these authors. On the other hand, the dimensions of the tricarinate and eroded specimens assigned to *C. pavillieri* by Wiese (1997) reveal that their taxonomical classification may be erroneous, as Meister and Abdallah (2005) suggested.

Concerning its phylogeny, there is thus no doubt that this species is closely linked to *C. (C.) quaasi*, and that *C. (C.) pavillieri* may be evolved from the Peron's species by a reduction of the whorl breadth and the umbilical width.

Occurrence: It occurs in the lower Turonian of Tunisia, Egypt, Madagascar, France, Spain, Israel, the USA, Romania and, possibly, Algeria and Nigeria, in biostratigraphic units equivalent to the upper half of the *Watinoceras devonense* zone and to the *Mammites nodosoides* zone. Within the Iberian Trough, records of *C. (C.) pavillieri* have been obtained in the upper part of the *Choffaticeras (Choffaticeras) quaasi* zone and in the *Spathites (Ingridella) malladae* subzone of the Inner Castilian Platform. Furthermore, Lamolda et al. (1989, 1997) and Santamaría-Zabala (1991, 1995) also identified this species in the lower Turonian of the Outer Navarro-Cantabrian Platform.

Choffaticeras (Choffaticeras) segne (Solger, 1903)

Figs. 5(5) and 6(1–3)

1903. *Pseudotissotia segnis* – Solger, p. 77, Pl. 4, Figs. 1, 2; Text-Figs. 16–21.

1907. *Pseudotissotia (Choffaticeras) segnis* Solger – Pervinquière, p. 351, Pl. 23, Figs. 1a, b, 2a, b [non Fig. 3, var. *discoidalis* (= *C. (C.) quaasi*)].

?1909. *Tissotia schweinfurthi* – Eck, p. 184, Figs. 6–8.

1912. *Leoniceras segne* (Solger) – Douvillé, p. 313, Text-Fig. 49.

?1914. *Pseudotissotia segnis* Solger – Eck, p. 204, Pl. 15, Fig. 3; Pl. 16, Figs. 1–3; Text-Figs. 10–20.

1915. *Pseudotissotia (Choffaticeras) segnis* Solger – Greco, p. 213, Pl. 18, Fig. 5a, b; Pl. 19, Fig. 1a, b; Text-Fig. 4.

1920. *Pseudotissotia segnis* Solger – Taubenhaus, p. 41, Pl. 4, Figs. 3a, b, 5; Pl. 6, Fig. 4 [non Pl. 4, Figs. 1a, b, 2, var. indet.; Pl. 4, Fig. 4a, b, *macrodiscus* (= *C. (C.) quaasi*); Pl. 7, Fig. 4, *obesa* (? = *C. (C.) douvillei*)].

?1928. *Leoniceras segne* (Solger) – Douvillé, p. 26, Pl. 5; Text-Figs. 16, 17.

cf. 1937. *Pseudotissotia (Leoniceras)* cf. *segne* Solger – Basse, p. 187.

1940. *Leoniceras segne* (Solger) – Basse, p. 460, Pl. 9, Fig. 1a–c.

non 1951. *Leoniceras segne* (Solger) – Faraud, p. 155, Text-Fig. 2 (= *C. (C.) quaasi*).

cf. 1960. *Choffaticeras (Leoniceras)* cf. *segne* (Solger) – Wiedmann, pp. 712, 716, 721, 723.

cf. 1964. *Choffaticeras (Leoniceras)* cf. *segne* (Solger) – Wiedmann, pp. 111–112, 115–116.

1969. *Choffaticeras segne* (Solger) – Freund and Raab, p. 54, Text-Fig. 10j–l.

cf. 1975b. *Choffaticeras (Leoniceras)* cf. *segne* (Solger) – Wiedmann, p. 141.

cf. 1978. *Leoniceras* cf. *segne* (Solger) – Wiedmann and Kauffman, p. 2.

cf. 1979. *Leoniceras* cf. *segne* (Solger) – Wiedmann, pp. 176, 199.

1982. *Leoniceras segne* (Solger) – Segura and Wiedmann, p. 299, Pl. 1, Figs. 3, 4.

cf. 1982. *Leoniceras* cf. *segne* (Solger) – Segura and Wiedmann, p. 299, Pl. 2, Figs. 6, 7.

1982. *Leoniceras segne* (Solger) – Carretero-Moreno, p. 271.

?1984. *Leoniceras segne* (Solger) - Meléndez-Hevia, p. 113, Pl. 19, Fig. 1a, b.

1992. *Choffaticeras segne* (Solger) – Thomel, p. 236, Pl. 129, Figs. 1–3.

1994. *Choffaticeras (Choffaticeras) segne* (Solger) – Chancellor et al., p. 88.

aff. 2005. *Choffaticeras* aff. *segne* (Solger) – Meister and Abdallah, p. 140, Pl. 22, Fig. 1.

Type: The lectotype designated by Chancellor et al. (1994) is the original of Solger (1903: p. 77, Pl. 4, Figs. 1, 2) from the lower Turonian of Wadi Mor, Egypt.

Material and dimensions:

	D	*H* (%)	*B* (%)	*U* (%)
MS-5	1200	613 (51)	410 (34)	205 (17)
MS-9	2180	924 (42)	710 (33)	518 (24)

Description: Involute discoidal forms with little compressed whorl section ranging from suboval to subtrapezoidal, and rounded tricarinate venter. During juvenile stages, there can arise up to 40 rectiradiate or slightly prorsiradiate ribs per whorl that become more pronounced at the ventrolateral margin and weaken approaching the umbilicus, as well as several umbilical tubercles. The ornamentation progressively disappears during ontogeny. Adult specimen lacks keels, giving rise to a rounded ventral region. The suture lines are variable with quite shallow first lateral lobes divided into two branches of different length.

Discussion: The whorl section is proportionally wider, the keel slightly more marked and the umbilicus wider than that of the type species, *Choffaticeras (Choffaticeras) meslei* (Peron, 1897). Identifying *C. (C.) segne* may, however, be very difficult because its dimensions are notably variable, as was noticed by Pervinquière (1907), Eck (1910) and Taubenhaus (1920). Douvillé (1928) highlighted the presence of striking umbilical tubercles on the inner whorls as being the most significant feature of this species. Nevertheless, the limits of *C. (C.) segne* with the close species are artificial, because some characteristics change in a continuous manner, as pointed out by Freund and Raab (1969).

In 1907, Pervinquière described *Pseudotissotia (C.) segnis* Solger var. *discoidalis*. On the basis of the work of Freund and Raab (1969), this taxon was considered a synonym of *C. (C.) quaasi* (Peron, 1904), as justified above in the discussion concerning this species. Moreover, these authors elevated *P. segnis* var. *obesa* Taubenhaus, 1920, to specific status, including *Vascoceras (Pachyvascoceras) triangulare* Faraud, 1940, *Discovascoceras tesselitense* Collignon, 1957, and *D. defrennei* Collignon, 1957, in its synonymy. In reality, the fragment of the depressed subtriangular and relatively evolute body chamber illustrated as *P. segnis* var. *obesa* by Taubenhaus (1920: Pl. 7, Fig. 4) should, however, probably be assigned to *C. (C.) douvillei*. Likewise, Freund and Raab (1969) stated that *Tissotia schweinfurthi* Eck, 1909, could be considered a transitional form between *C. (C.) segne* and *C. (C.) securiforme* (Eck, 1909). According to these authors, the specimens of *Leoniceras* gr. *segne* of Roman and Mazeran (1913: p. 28, Pl. 3, Fig. 3), of *Pseudotissotia segnis* of Eck (1914: p. 204, Pl. 16, Figs. 1, 2) and of *Leoniceras segne* of Douvillé (1928: p. 27, Pl. 5a, b) also develop concave flanks and, therefore, a morphology close to *T. schweinfurthi*. For this reason, Freund and Raab (1969) assigned with doubts the specimens of Roman and Mazeran (1913) and Douvillé (1928) to *C. (C.) securiforme*. They considered *T. schweinfurthi* as a probable synonym of *C. (C.) segne* and maintained that the ammonites of Eck (1914) could be possible members of Solger's species. In our opinion, the morphology of *T. schweinfurthi* probably coincides with specimens of *C. (C.) segne* closer to *C. (C.) securiforme*. Likewise, the ammonites of Eck (1914) and Douvillé (1928) bear great resemblance to ones assigned to *C. (C.) segne* by Meléndez-Hevia (1984) and have ventral regions, ventrolateral grooves and whorl breadths, whose features and dimensions resemble those of typical *C. (C.) securiforme*. However, they show an umbilicus that is proportionally narrower than that of this species. It can be thus stated that the specimens of Eck (1914), Douvillé (1928) and Meléndez-Hevia (1984) seem to correspond to intermediate forms

between *C. (C.) segne* and *C. (C.) securiforme*. Recently, Kassab (1985, 1991, 1994) and Kassab and Obaidalla (2001) proposed *C. luciae*, *C. pavillieri*, *C. schweinfurthi*, *C. securiforme* and, doubtfully, *C. quaasi* as synonyms of *C. segne*. In fact, they assigned to the latter some non contemporary species with very different morphologies that are even attributable to different subgenera.

Occurrence: Lower Turonian of Egypt, Tunisia, Jordan, Syria, Spain, Israel and France. In the Iberian Trough, members of *C. (C.) segne* have been cited in the *Choffaticeras (Chofaticeras) quaasi* and the *Spathites (Ingridella) malladae* zones of the South-Ebro Area and the Central Sector, although the original stratigraphical levels of the specimens presented herein have not could be determined.

Choffaticeras (Choffaticeras) sinaiticum (Douvillé, 1928)
Figs. 6(4, 5) and 7(1)

?1907. *Pseudotissotia (Choffaticeras) luciae* var. *stricta* – Pervinquière, p. 355.

?1915. *Pseudotissotia (Choffaticeras) destefanii* – Greco, p. 217, Pl. 20; Text-Fig. 6.

?1915. *Pseudotissotia (Choffaticeras) segnis* Solger var. *discoidalis* Pervinquière – Greco, p. 214, Pl. 19, Figs. 2, 3.

1928. *Leoniceras sinaiticum* – Douvillé, p. 25, Pl. 4, Fig. 4a, b.

1969. *Choffaticeras sinaiticum* (Douvillé) – Freund and Raab, p. 58, Text-Fig. 11e–h.

1984. *Leoniceras discoidale* (Pervinquière) – Meléndez-Hevia, Pl. 14, Fig. 1a, b [only].

1992. *Choffaticeras sinaïticum* [sic] (Douvillé) – Thomel, p. 236, Pl. 123, Figs. 1, 2; ?Pl. 124, Figs. 1–3; Pl. 125; Pl. 128, Figs. 1, 2, 7; Pl. 129, Fig. 4.

? aff. 1996. *Choffaticeras* aff. *sinaiticum* (Douvillé) – Meister and Abdallah, p. 15, Pl. 10, Fig. 1; Text-Fig. 6e.

2005. *Choffaticeras sinaiticum* (Douvillé) – Meister and Abdallah, p. 139, Pl. 21, Figs. ?1, 2; Text-Fig. 27.

cf. 2005. *Choffaticeras* cf. *sinaiticum* (Douvillé) – Meister and Abdallah, p. 140, Pl. 20, Fig. 2.

Type: Without designation.

Material and dimensions:

	D	*H* (%)	*B* (%)	*U* (%)
CB-R-544	1210	822 (68)	rv390 (32)	rv260 (21)
CB-R-555	rv692	rv350 (51)	rv176 (25)	rv55 (8)
FT-R-702	rv900	rv560 (62)	rv182 (20)	rv62 (7)
TA-R-427	971	492 (51)	186 (19)	116 (12)
TA-R-854	1293	600 (46)	rv299 (23)	219 (17)
TA-R-93	601	340 (57)	129 (21)	67 (11)
TE-S-136	2170	975 (45)	460 (21)	300 (14)

Description: Compressed and involute discoidal specimens. Subogival or subtriangular whorl sections with strongly sharpened ventral regions, slightly convex or almost flat flanks, reaching their greatest breadth on their inner third, and narrow umbilici with subvertical walls. The ornamentation is almost non-existent, although some smaller specimens seem to bear about 35 weak ribs per whorl on the outer half of the flanks that rapidly disappear. The umbilici broaden during ontogeny and their margins become rounded and weaken to be hardly distinguishable. The suture lines are the typical of the subgenus, variable and with asymmetrical first lateral lobes.

Discussion: Its features are clearly transitional between the subgenera *Choffaticeras (Choffaticeras)* Hyatt, 1903, and *Choffaticeras (Leoniceras)* Douvillé, 1912, but it has been here decided to refer this species to the first group, as it shows a tricarinate ventral region during the first ontogenetic stages, although it soon becomes monocarinate. Likewise, the general shape is very similar to that of typical *C. (C.) pavillieri* (Pervinquière, 1907) and it cannot be rejected that *C. (C.) sinaiticum* might be a mere synonym. The non illustrated ammonites differentiated by Pervinquière (1907: p. 355) as belonging to his new *Pseudotissotia (C.) luciae* var. *stricta* have been regarded as possible specimens of *C. (C.) sinaiticum* by Freund and Raab (1969). The dimensions of these specimens, which have not been located in the MNHN, are close to those of *C. (C.) sinaiticum*. These authors also indicated that the description of *P. (C.) destefanii* Greco, 1915, is based on a specimen of *C. (C.) sinaiticum* with a flat venter by damage of the ventral region. In fact, it seems that the type of *P. (C.) destefanii* cannot be distinguished from *C. (C.) sinaiticum*, except for the rare form of its apparently eroded venter. Likewise, Freund and Raab (1969) attributed two of the three specimens classified by Greco (1915: Pl. 19, Figs. 2, 3) as belonging to *Pseudotissotia (Choffaticeras) segnis* var. *discoidalis* Pervinquière, 1907, to the species of Douvillé. Although Greco (1915) did not provide any dimensions of these ammonites, it can be observed on his illustrations that, despite their reduced size, both maintain conspicuous siphonal keels, whereas the lateral keels have almost disappeared, due to which they could also be specimens of *C. (C.) sinaiticum*. Finally, it should be emphasized that the specimen of Thomel (1992: Pl. 124) presents a quite rounded ventral region, and that the ammonites of Meister and Abdallah (1996: Pl. 10, Fig. 1, Text-Fig. 6e; 2005, Pl. 21, Fig. 1) show dimensions close to *C. (L.) luciae*, although both forms could possibly be included within the variability of *C. (C.) sinaiticum*, which is still poorly known.

Although the members of this species are considerably scarce, the morphologies and distributions of them reveal that they bear great phylogenetical resemblance to *C. (C.) pavillieri*, from which *C. (C.) sinaiticum* seems to be derived.

Occurrence: Lower Turonian of Egypt, Israel, Spain, France and Tunisia. It seems that the presence of this species in the Iberian Trough is restricted to the upper levels of the *Spathites (Ingridella) malladae* subzone of the Guadarrama Area.

Choffaticeras (Leoniceras) Douvillé, 1912

Type species: *Pseudotissotia (Choffaticeras) luciae* Pervinquière, 1907, by original designation.

Diagnosis: Lanceolate whorl sections without tubercles or ventrolateral keels during none of the ontogenetic stages. The flanks tend to become slightly concave on their outer half.

Discussion: Douvillé (1912) established the genus *Leoniceras* for the species of *Choffaticeras* Hyatt, 1903, wich show asymmetrical lateral lobes, and considered that this group is very close to Coilopoceratidae Hyatt, 1903. Subsequently, other

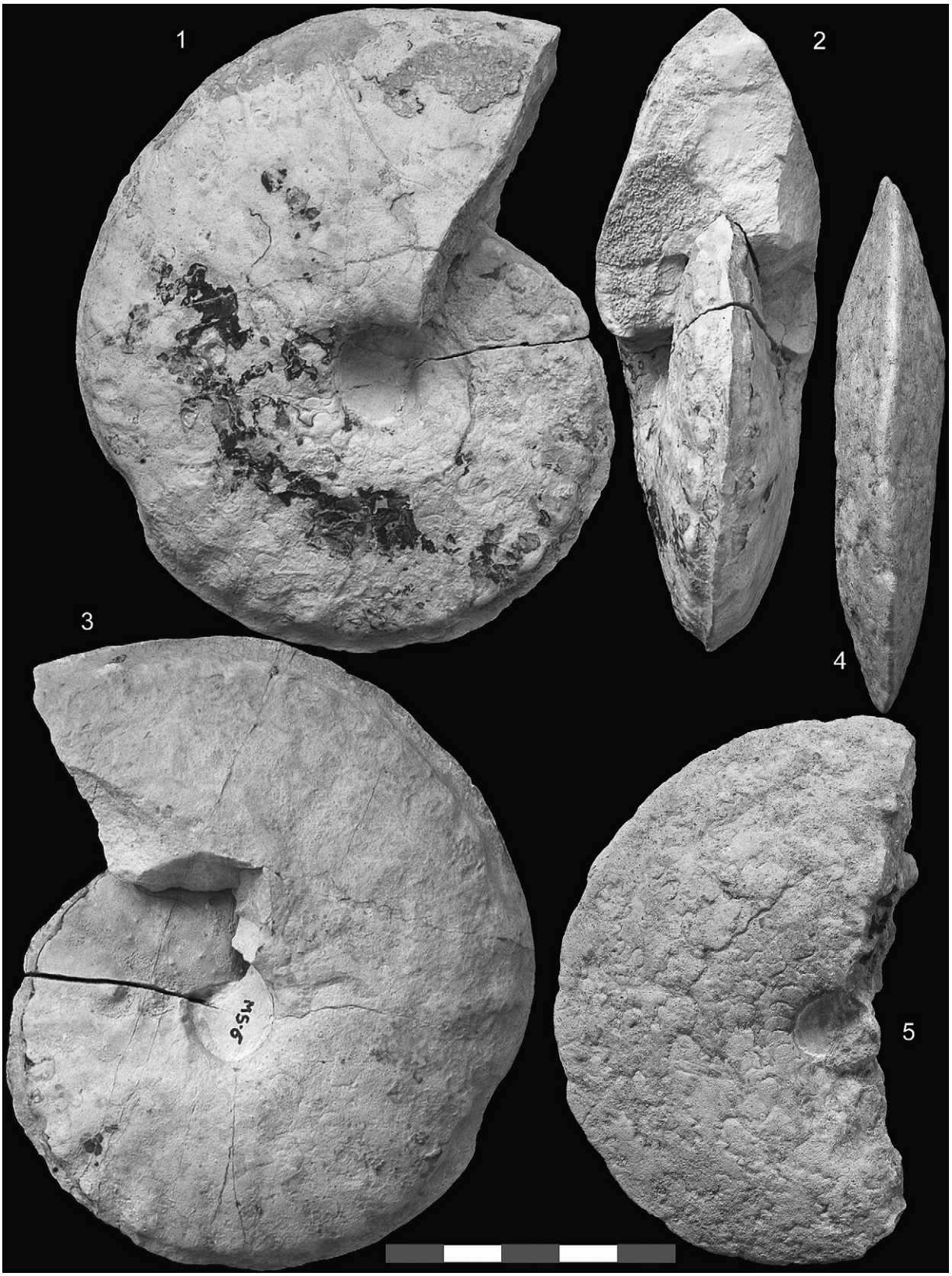

Fig. 6. 1, 2, 3. *Choffaticeras (Choffaticeras) segne* (Solger, 1903), specimen MS-5, × 1. 1. Lateral view. 2. Apertural view. 3. Lateral view. 4, 5. *Choffaticeras (Choffaticeras) sinaiticum* (Douvillé, 1928), specimen TA-R-427, from the *Spathites (Ingridella) malladae* subzone of Tamajón, × 1. 4. Ventral view. 5. Lateral view.
Fig. 6. 1, 2, 3. *Choffaticeras (Choffaticeras) segne* (Solger, 1903), spécimen MS-5, × 1. 1. Vue latérale. 2. Vue aperturale. 3. Vue latérale. 4, 5. *Choffaticeras (Choffaticeras) sinaiticum* (Douvillé, 1928), spécimen TA-R-427, de la sous-zone à *Spathites (Ingridella) malladae* de Tamajón, × 1. 4. Vue ventrale. 5. Vue latérale.

investigators, such as Douvillé (1928), Roman (1938), Basse (1940), Faraud (1951), Basse (1952), Freund (1959) and Collignon (1957, 1965), opted for maintain the genus *Leoniceras*, following the taxonomical classification suggested in the original description of this group. Other authors preferred to consider it as a mere subgenus of *Pseudotissotia* Peron, 1897.

Nevertheless, after checking the description of Douvillé, Reyment (1955) regarded that maintaining a distinction based on the suture line is not adequate, and established the group *Choffaticeras (Leoniceras)* for the monocarinate forms of the genus. Freund and Raab (1969), Cobban and Scott (1972), Santamaría-Zabala (1991, 1995), Thomel (1992), Meister and Abdallah (1996) and Amédro et al. (1996), amongst others, preferred not to divide the genus *Choffaticeras*, considering *Leoniceras* as a synonym.

On the basis of the proximity and undeniable phylogenetic relationship that links this subgenus to *C.* (*Choffaticeras*), we agree with the classical interpretation of Reyment (1955), maintained by Wright in Moore (1957) and, after studying the Spanish specimens, as well by Wiedmann (1960, 1964), and recently supported by Chancellor et al. (1994), Kennedy (1994) and Wright in Kaesler (1996), by whom it is placed within *Choffaticeras* as a subgenus.

Due to the absence of a general revision, organizing and establishing possible synonymous forms, this group probably has too many species.

Occurrence: It has a geographical distribution similar to the genus. Its temporal distribution, however, seems to begin shortly after that of the subgenus *C.* (*Choffaticeras*).

Choffaticeras (Leoniceras) luciae (Pervinquière, 1907)
Fig. 7(2–4)

1907. *Pseudotissotia (Choffaticeras) luciae* – Pervinquière, p. 354, Pl. 24, Figs. 1, 2; Text-Figs. 135–137.

non 1907. *Pseudotissotia (Choffaticeras) luciae* var. *stricta* – Pervinquière, p. 355 (? = *C. (C.) sinaiticum*).

1912. *Leoniceras luciae* (Pervinquière) – Douvillé, p. 311, Text-Fig. 51.

?1915. *Pseudotissotia (Choffaticeras) mokattanica* – Greco, p. 215, Pl. 19, Fig. 5; Text-Fig. 5.

1940. *Leoniceras luciae* (Pervinquière) – Basse, p. 459.

1940. *Leoniceras luciae* (Pervinquière) – Fabre, p. 295, Pl. 9, Figs. 3, 4; Text-Figs. 47, 48.

?1951. *Leoniceras luciaeformis* – Faraud, p. 152, Pl. 5, Figs. 2–4; Text-Fig. 3.

1957. *Choffaticeras (Leoniceras) luciae* (Pervinquière) – Wright in Moore, p. L424, Text-Fig. 543/1a–c

cf. 1960. *Choffaticeras (Leoniceras)* cf. *luciae* (Pervinquière) – Wiedmann, pp. 714, 723.

cf. 1964. *Choffaticeras (Leoniceras)* cf. *luciae* (Pervinquière) – Wiedmann, pp. 111, 116.

1965. *Leoniceras luciae* (Pervinquière) – Collignon, p. 191, Text-Fig. 8a, b.

1969. *Choffaticeras luciae trisellatum* – Freund and Raab, p. 59, Pl. 9, Figs. 7, 8; Text-Figs. 12i–q, 13a–h.

cf. 1975b. *Choffaticeras (Leoniceras)* cf. *luciae* (Pervinquière) – Wiedmann, p. 142.

cf. 1979. *Leoniceras* cf. *luciae* (Pervinquière) – Wiedmann, p. 199.

1981. *Leoniceras luciae* (Pervinquière) – Amard et al., p. 57, Pl. 10, Fig. 6a, b.

1984. *Choffaticeras quaasi* (Peron) – Meléndez-Hevia, Pl. 12, Fig. 2 [only].

1984. *Leoniceras discoidale* (Pervinquière) – Meléndez-Hevia, Pl. 13, Fig. 2 [only].

1984. *Leoniceras barjonai* (Choffat) – Meléndez-Hevia, Pl. 17, Fig. 2a, b [only].

1984. *Leoniceras luciae* (Pervinquière) – Meléndez-Hevia, p. 113, Pl. 17, Fig. 1a, b; Pl. 18, Fig. 1.

1990. *Choffaticeras luciae* (Pervinquière) – Robaszynski et al., p. 268, Pl. 23, Fig. 1a, b; Pl. 24, Fig. 1a, b.

1992. *Choffaticeras luciae* (Pervinquière) – Thomel, p. 234, Pl. 127, Figs. 1, 2.

? aff. 1992. *Choffaticeras* aff. *mokattanicum* (Greco) – Thomel, p. 235, Pl. 126.

1994. *Choffaticeras (Leoniceras) luciae* (Pervinquière) – Chancellor et al., p. 91, Pl. 25, Figs. 1–3.

1994. *Choffaticeras (Leoniceras) luciae* (Pervinquière) – Kennedy, p. 262.

1996. *Choffaticeras luciae* (Pervinquière) – Meister and Abdallah, p. 15, Pl. 13, Figs. 1a, b, 3.

1996. *Choffaticeras (Leoniceras) luciae* (Pervinquière) – Wright in Kaesler, p. 176, Text-Fig. 139/2a–c.

?1997. *Choffaticeras luciae* (Pervinquière) – Wiese, Pl. 1, Fig. 4.

2001. *Choffaticeras (Leoniceras) barjonai* (Choffat) – Callapez and Ferreira, p. 93, Pl. 14, Figs. 7, 8; Text-Figs. 24.1, 24.4–6.

2005. *Choffaticeras luciae* (Pervinquière) – Meister and Abdallah, p. 140, Pl. 22, Fig. 2; Pl. 23, Figs. 1–3.

Type: The holotype by original designation is the specimen of Pervinquière (1907: Pl. 24, Fig. 2), occurring in the lower Turonian of Ain Nakhla, Tunisia. Actually it is kept with the number J04253 in the MNHN, after having remained in the SP and the UPMC.

Material and dimensions:

	D	*H* (%)	*B* (%)	*U* (%)
862	1184	594 (50)	342 (29)	180 (15)
863	1990	rv970 (49)	rv525 (26)	rv335 (17)
CA-R-526	1215	666 (55)	318 (26)	162 (13)
CA-S-524	2210	1022 (46)	rv700 (32)	435 (20)
	1780	775 (44)	655 (37)	348 (20)
CA-S-525	1500	rv720 (48)	495 (33)	rv230 (15)
CB-R-23				
CB-R-549	rv1475	rv717 (49)	rv382 (26)	rv254 (17)
CG-R-534	1410	607 (43)	rv310 (22)	295 (21)
FV-R-853		rv800	rv620	330
		rv600	rv440	260
TA-R-428	2330	966 (41)	472 (20)	571 (25)
TA-R-62	1341	675 (50)	354 (26)	223 (17)
TA-R-63	1390	725 (52)	rv420 (30)	220 (16)
TA-S-61	1840	844 (46)	473 (26)	327 (18)
TA-S-71	1530	676 (44)	432 (28)	285 (19)
TE-S-137	1640	861 (53)	485 (30)	239 (15)
TE-S-75	rv1100	rv510 (46)	rv370 (34)	rv130 (12)

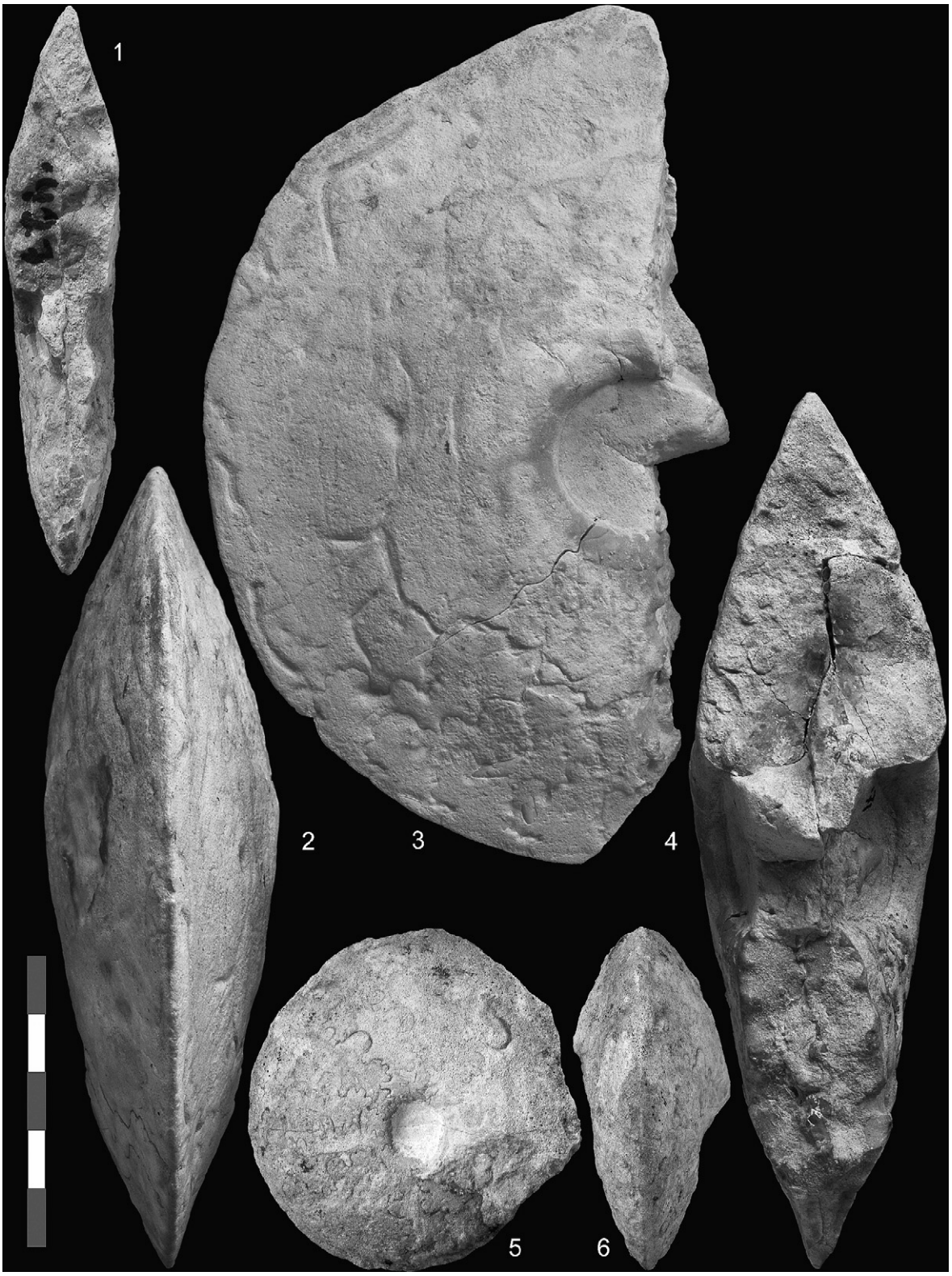

Fig. 7. 1. *Choffaticeras (Choffaticeras) sinaiticum* (Douvillé, 1928), specimen TA-R-427, from the *Spathites (Ingridella) malladae* subzone of Tamajón, apertural view, × 1. 2, 3, 4. *Choffaticeras (Leoniceras) luciae* (Pervinquière, 1907), specimen TA-S-71, from the *Choffaticeras (Leoniceras) luciae* subzone of Tamajón, × 1. 2. Ventral view. 3. Lateral view. 4. Apertural view. 5, 6. *Choffaticeras (Leoniceras) barjonai* (Choffat, 1898), specimen CA-R-186, from the *Choffaticeras (Leoniceras) luciae* subzone of Condemios, × 1. 5. Lateral view. 6. Ventral view.

Fig. 7. 1. *Choffaticeras (Choffaticeras) sinaiticum* (Douvillé, 1928), spécimen TA-R-427, de la sous-zone à *Spathites (Ingridella) malladae* de Tamajón, vue aperturale, × 1. 2, 3, 4. *Choffaticeras (Leoniceras) luciae* (Pervinquière, 1907), spécimen TA-S-71, de la sous-zone à *Choffaticeras (Leoniceras) luciae* de Tamajón, × 1. 2. Vue ventrale. 3. Vue latérale. 4. Vue aperturale. 5, 6. *Choffaticeras (Leoniceras) barjonai* (Choffat, 1898), spécimen CA-R-186, de la sous-zone à *Choffaticeras (Leoniceras) luciae* de Condemios, × 1. 5. Vue latérale. 6. Vue ventrale.

Description: Monocarinate and involute ammonites with lanceolate or compressed subtriangular section showing their greatest breadth close to the umbilical margins. Oxyconic specimens without ribs or tubercles and with slightly concave ventrolateral regions. The flanks are convex or flat on the inner two thirds, and the umbilici are small, with flat and vertical walls and blunt umbilical angles. Adult specimens reach large sizes, even surpassing diameters of 25 centimeters.

Discussion: The main distinguishing features of *Choffaticeras (Leoniceras) luciae* are the relatively broad umbilicus, the vertical umbilical wall, the subtriangular whorl section and the shallow ventrolateral groove drawn on the outer extreme of the flanks. *C. (L.) massipiana* (Pervinquière, 1907) presents a much more compressed shell with a broad umbilicus, a feeble ornamentation and a suture line with wide saddles on the flanks. The proportions and form of *C. (L.) philippii*, however, are very close to *C. (L.) luciae*, although their ribbing and suture lines are quite different. Additionally, *C. (C.) securiforme* (Eck, 1909), apart from having a tricarinate ventral region, possesses a narrow whorl and a broad umbilicus with concave and oblique wall and rounded margin. Although these features are rather different from those of typical *C. (L.) luciae*, some members of this species, like the ammonites of Amard et al. (1981: Pl. 10, Fig. 6a, b), Robaszynski et al. (1990: Pl. 24, Fig. 1a, b) and Meister and Abdallah (1996: Pl. 13, Figs. 1a, b, 3; 2005, Pl. 23, Fig. 3), can present a marked ventrolateral groove, probably caused by post mortem deformation, that make it difficult to identify them.

C. (L.) luciae shows a narrower whorl section and a smaller umbilical width than *C. (L.) barjonai* (Choffat, 1898). In spite of these differences, both species are very similar. In fact, after studying the monocarinate members of the genus, Freund and Raab (1969) stated the existence of intermediate forms between *C. (L.) luciae* and *C. (L.) barjonai*. On the basis of these transitional specimens, they described the subspecies *C. luciae trisellatum*, including morphologies with a whorl section and an umbilicus of intermediate dimensions. In view of this, as indicated by Robaszynski et al. (1990) and Meister and Abdallah (1996), it is necessary to examine the limits and relationship between *C. (L.) luciae* and *C. (L.) barjonai*.

Choffat (1898) noted that the body chambers of two of his specimens present feeble radial plications so-called ''dépressions radiantes'' by him, placed near to the keel. Pervinquière (1907), however, emphasized that the shells of his species present a smooth appearance. Although this feature may seem distinctive at first sight, it cannot be used for differentiating between the two taxa, as Basse (1940) noticed plications in some original specimens of Pervinquière (1907), and Freund and Raab (1969) described the ornamentation presented by their subspecies *C. luciae trisellatum*. Among the adult and juvenile *C. (L.) luciae* and *C. (L.) barjonai* studied herein, no ornamented specimens have been found. The same conclusion can be reached regarding most of the rest of the Spanish members of the genus, which are less ornamented than the specimens occurring in other geographical areas. In our opinion, although the practically continuous morphological variability that can be established between *C. (L.) luciae* and *C. (L.) barjonai* sometimes makes it difficult to distinguish both species, the latter seems to have a slightly higher vertical distribution that recommends maintaining their specific separation.

The few specimens attributed to the little-known *Pseudotissotia (C.) mokattanica* Greco, 1915, and *L. luciaeformis* Faraud, 1951, despite having a slightly smaller umbilical width than the typical *C. (L.) luciae*, they show whorl breadths and other features characteristic of this species. Therefore, these taxa of Greco and of Faraud may possibly be mere synonyms of *C. (L.) luciae*.

According to Faraud (1951: pp. 153, 157) both his new *L. luciaeformis* as well as *C. (L.) luciae* are forms close to the rare Syrian species *P. (L.) alaouitense* Basse, 1937. The same species was, however, included in the synonymy of *C. (C.) securiforme* (Eck, 1909) by Freund and Raab (1969). In fact, the lectotype of the taxon of Basse, which is presently kept in the MNHN and that has been designated and refigured in the present work (Fig. 8(1, 2)), seems to be a compressed specimen of *C. (C.) securiforme*.

Pervinquière (1907: p. 355) differentiated some of his non illustrated specimens as belonging to his new *P. (C.) luciae* var. *stricta*. Subsequently, Freund and Raab (1969) considered that these specimens may possibly be attributable to *C. (C.) sinaiticum*.

The small size and marked ornamentation of the specimen of *C. luciae* of Wiese (1997) make its taxonomical classification considerably doubtful, as Meister and Abdallah (2005) recently suggested. The dimensions of the ammonites classified as *C. (L.) barjonai* by Callapez and Ferreira (2001: p. 93) demonstrate that the figured specimens must be assigned to the species of Pervinquière and that some of the non illustrated ones could be considered members of the species of Choffat.

The origin of *C. (L.) luciae* seems to be among the most compressed and sharpened members of *Choffaticeras (Choffaticeras)* Hyatt, 1903, specifically of *C. (C.) sinaiticum*, by loss of the ventrolateral keels and progressive increase of the whorl breadth and umbilical width.

Occurrence: This species has been cited in the lower Turonian of Tunisia, Syria, France, Spain, Israel, Algeria and, with doubts, Egypt. Specimens of *C. (L.) luciae* have been obtained within the Iberian Trough in the lower part of the eponymous subzone of the Central Sector and, although uncertain, the South-Ebro Area. In Tunisia, Robaszynski et al. (1990) identified *C. (L.) luciae* in the immediately previous biostratigraphic unit to the *Mammites nodosoides* zone, and Meister and Abdallah (1996) determined the same interval by means of this species of Pervinquière. In Israel, Freund and Raab (1969) used *C. luciae trisellatum* as index of a lower Turonian zone.

Choffaticeras (Leoniceras) barjonai (Choffat, 1898)

Figs. 7(5, 6) and 9(1–4)

1898. *Pseudotissotia barjonai* – Choffat, p. 73, Pl. 3; Pl. 18, Fig. 3; Pl. 22, Figs. 40–42.

1951. *Leoniceras barjonai* (Choffat) – Faraud, p. 151, Text-Fig. 5.

Fig. 8. 1, 2. Here designated lectotype of *Pseudotissotia (Leoniceras) alaouitense* Basse, 1937, specimen R52529 of the MNHN, from the lower Turonian of Ain Tineh, Syria, × 1. 1. Apertural view. 2. Lateral view. 3, 4, 5. The lectotype of *Pseudotissotia barjonai* Choffat, 1898, specimen 845 of the SGP, from the lower Turonian of Moinho-do-Almoxarife, Portugal, × 1. 3. Ventral view. 4. Lateral view. 5. Apertural view.

Fig. 8. 1, 2. Lectotype désigné ici de *Pseudotissotia (Leoniceras) alaouitense* Basse, 1937, spécimen R52529 déposé au MNHN, provenant du Turonien inférieur de Ain Tineh, Syrie, × 1. 1. Vue aperturale. 2. Vue latérale. 3, 4, 5. Le lectotype de *Pseudotissotia barjonai* Choffat, 1898, spécimen 845 déposé dans les SGP, du Turonien inférieur de Moinho-do-Almoxarife, Portugal, × 1. 3. Vue ventrale. 4. Vue latérale. 5. Vue aperturale.

1960. *Choffaticeras (Leoniceras) barjonai* (Choffat) – Wiedmann, pp. 714, 723.

1964. *Choffaticeras (Leoniceras) barjonai* (Choffat) – Wiedmann, pp. 111, 116.

1975b. *Choffaticeras (Leoniceras) barjonai* (Choffat) – Wiedmann, p. 142.

? cf. 1978. *Leoniceras* cf. *barjonai* (Choffat) – Wiedmann and Kauffman, Pl. 9, Fig. 3.

? cf. 1979. *Leoniceras* cf. *barjonai* (Choffat) – Wiedmann, p. 199, Pl. 9, Fig. 3.

1984. *Leoniceras barjonai* (Choffat) – Meléndez-Hevia, p. 111, Pl. 15, Fig. 1; Pl. 16, Fig. 1a, b [only].

non 2001. *Choffaticeras (Leoniceras) barjonai* (Choffat) – Callapez and Ferreira, p. 93, Pl. 14, Figs. 7, 8; Text-Figs. 24.1, 24.4-6 (= *C. (L.) luciae*).

Type: Choffat described five specimens in his work, but he did not designate a holotype. Two of the original ammonites are kept in the SGP. The specimen 845 illustrated by Choffat (1898: Pl. 3; Pl. 22, Fig. 40) from the lower Turonian of Moinho-do-Almoxarife, Portugal, is the best preserved one. It was designated as lectotype by Callapez and Ferreira (2001), with which we agree, and has been here refigured (Fig. 8 (3–5)).

Material and dimensions:

	D	*H* (%)	*B* (%)	*U* (%)
CA-R-186	632	324 (51)	268 (42)	80 (13)
CA-R-407	1530	672 (44)	rv520 (34)	295 (19)
CA-R-500	1346	670 (50)	rv575 (43)	210 (16)
CA-R-861	1950	690 (35)	480 (25)	435 (22)
	1700	650 (38)	500 (29)	370 (22)
	1560	659 (42)	495 (32)	346 (22)
CB-R-551	1495	699 (47)	594 (40)	rv325 (22)
CG-R-513	2210	823 (37)	733 (33)	574 (26)
CG-S-670	2490	920 (37)	670 (27)	768 (31)
	2160	862 (40)	754 (35)	626 (29)
TA-R-135	2000	742 (37)	610 (31)	500 (25)
TA-R-759	rv1650	rv782 (47)	rv540 (33)	rv280 (17)
TA-S-139		805	509	rv498
TA-S-140	rv1700	rv670 (39)	rv430 (25)	rv330 (19)
TA-S-411	1830	864 (47)	635 (35)	339 (19)
TA-S-53	1950	715 (37)	rv480 (25)	548 (28)
	1780	745 (42)	rv565 (32)	404 (23)
		732	555	rv275
TA-S-68	2050	890 (43)	540 (26)	500 (24)
	1850	830 (45)	540 (29)	370 (20)
	1720	734 (43)	585 (34)	356 (21)
TA-S-70		748	490	rv320
TE-S-138	1780	650 (37)	rv530 (30)	rv465 (26)

Description: Discoidal ammonites with slightly broader whorl sections than most of the members of this subgenus. They present sharp ventral regions with keels, convex flanks that can become flat approaching the ventrolateral zones, and moderately broad and deep umbilici with flat or slightly concave walls. The whorls are very characteristic with heart-shaped or sublanceolate sections, reaching their greatest breadth on the inner third of the flanks and slightly decreasing their breadth near the umbilical margins. Their suture lines show three lobes on the flanks and wide saddles. From the third lobe on, the sutures slightly vary the direction followed up to that point (Fig. 9).

Discussion: This species can easily be identified by its typical whorl section and the wide curvature of its umbilical slope. In his original description, Choffat (1898) compared this taxon with the tricarinate species *Pseudotissotia meslei* Peron, 1897, stating that they have very distinct morphological features. As already has been mentioned above, *C. (L.) barjonai* presents a wider and more heart-shaped whorl section than *C. (L.) luciae* (Pervinquière, 1907). Furthermore, the typical suture line of the latter species is more elevated and shows one element more, on account of which it can be distinguished from *C. (L.) barjonai*.

The notable morphological resemblance between *C. (L.) luciae* and *C. (L.) barjonai* and the higher vertical distribution of the latter species are very significant. These facts apparently reveal that *C. (L.) barjonai* could have arisen from *C. (L.) luciae* by small differences in the whorl section and the degree of involution, as well as by simplification of the suture line. Therefore, *C. (L.) barjonai* seems to be a specialized species adapted to slightly shallower and more restricted marine environments than *C. (L.) luciae*.

Occurrence: Lower Turonian of Portugal, France and Spain. Choffat (1898) found his species in the *Inoceramus labiatus* bed of Portugal that, as he indicated in page 44 of his work, is included in the K-L stratigraphic levels, which also contain the ammonites named ‘‘*Vascoceras* globulaires’’ by him. In the Iberian Trough, the specimens of *C. (L.) barjonai* have been collected from the upper part of the *Choffaticeras (Leoniceras) luciae* subzone of the Guadarrama Area. Likewise, Wiedmann (1960, 1964) obtained some specimens in probably equivalent levels of the South-Ebro Area.

Wrightoceras Reyment, 1954.

[*Imlayiceras* Leanza, 1967, p. 196, type species by original designation *Imlayiceras washbournei* Leanza, 1967. *Herrickiceras* Cobban and Hook, 1980, p. 22, type species by original designation *Placenticeras costatum* Herrick and Johnson, 1900].

Type species: *Bauchioceras (Wrightoceras) wallsi* Reyment, 1954, by original designation.

Diagnosis: Involute and compressed shells, with subogival, subrectangular or subtriangular whorl sections, and parallel or slightly convex flanks. The venters, which are flat, tabulate or concave and show sharp ventrolateral keels in the inner whorls, usually become rounded during ontogeny. Mature specimens lack ornamentation, although at young stages they can present small ventrolateral tubercles and plications or fine radial ribs that grow from the umbilicus and become progressively subdued until their total disappearance on the outer part of the flanks. The suture lines have many very simplified elements.

Discussion: Pervinquière (1907) modified the definition of the genus *Hoplitoides* von Koenen, 1898, in order to include his new species *H. munieri* in it, which maintains a tabulate ventral region throughout growth. In the same work, he also remarked that this feature corresponds to slightly older specimens than the typical *Hoplitoides*, whose juvenile flat venter disappears

Fig. 9. *Choffaticeras (Leoniceras) barjonai* (Choffat, 1898), specimen TA-S-68, from the *Choffaticeras (Leoniceras) luciae* subzone of Tamajón, × 4/7. 1. Apertural view. 2, 3. Lateral views. 4. Ventral view.

Fig. 9. *Choffaticeras (Leoniceras) barjonai* (Choffat, 1898), spécimen TA-S-68, de la sous-zone à *Choffaticeras (Leoniceras) luciae* de Tamajón, × 4/7. 1. Vue aperturale. 2, 3. Vue latérales. 4. Vue ventrale.

during ontogeny. Several years later, Reyment (1954) proposed *Wrightoceras* as a subgenus of his new group *Bauchioceras*, but in 1955 he regarded both taxa as subgenera of *Pseudotissotia* Peron, 1897, and remarked on the need, as already pointed out by Kummel and Decker (1954), of establishing a taxonomical group with generic status. Except in few works, as the presented by Wiedmann (1975b), *Wrightoceras* was considered a mere subgenus of *Pseudotissotia* until the publication of the paper of Kennedy et al. (1979). After observing that the specimens of *Ammonites galliennei* d'Orbigny, 1850, the type species of *Pseudotissotia*, are smooth and tricarinate during the first ontogenetic stages, in contrast to the members of *Wrightoceras*, these authors separated the taxon of Reyment as a distinct genus. This decision was accepted by many subsequent authors.

Chancellor (1982) highlighted that the suture line of *Imlayiceras washbournei* Leanza, 1967, seems unrecognisable, whereas the constrictions presented by the members of this species during the first ontogenetic stages, do not seem to be significant enough for maintaining this taxon as a genus. Kennedy et al. (1987) noted that *I. washbournei* bears great resemblance to *W. munieri*, differing from this species only in having tiny tubercles and fine constrictions on its first whorls. Therefore, these authors, as well as Chancellor (1982), included *Imlayiceras* in the synonymy of *Wrightoceras*, whereas Zaborski (1987) only regarded this possibility as probable. Moreover, Wright in Kaesler (1996) considered that the falcoid ribbing of *Herrickiceras* Cobban and Hook, 1980, is not a sufficiently significant feature for establishing a separate genus. According to all these observations, *Imlayiceras* and *Herrickiceras* have been here maintained as synonyms of *Wrightoceras*.

During the discussion on *Wrightoceras*, Reyment (1954, 1955) included within it the species *Bauchioceras (W.) wallsi* Reyment, 1954, *H. munieri*, *H. mirabilis* Pervinquière, 1907, *P. llareni* Karrenberg, 1935, and *P. gagnieri* Faraud, 1951. Freund and Raab (1969) considered that the suture line of *H. inca* Benavides-Cáceres, 1956, lacks the typical features of Coilopoceratidae Hyatt, 1903, due to which they considered it more adequate to assign it to *Wrightoceras*. Later, Wiedmann (1975b) described *W. submunieri*, and Amard et al. (1981) *W. reymenti*. In both cases, these species were referred to the genus *Wrightoceras* by their respective authors. Furthermore, Chancellor (1982), as opposed to Reyment (1954, 1955), preferred to assign *H. mirabilis* to *Herrickiceras*. Zaborski (1987) considered *W. wallsi*, *W. inca*, *W. llarenai*, *W. submunieri*, *W. reymenti* and *W. munieri* as species included in the genus, and regarded *W. mirabilis* as a synonym of the latter. He also indicated that *P. gagnieri* may possibly be included in *Wrightoceras*. Kennedy et al. (1987) recognized the specific status of *W. mirabilis* and included *W. inca* in the synonymy of *W. munieri*. Likewise, they pointed out that *Imlayiceras* might be a synonym of *Wrightoceras*. Finally, Chancellor et al. (1994) also cited *W. gagnieri*, considered a *nomen dubium* by them, as forming part of the genus. These authors maintained that the suture line of *H. mirabilis* resembles that of the family Coilopoceratidae more than that of Pseudotissotiidae. For this reason, they assigned this species to the genus *Hoplitoides*.

In relation to the phylogeny of the genus, Reyment and Chancellor (1978) regarded that the origin of the so-called ''*Hoplitoides* of Spain and of North-Africa'' is different to that of the authentic *Wrightoceras*. Moreover, Cobban and Hook (1980) indicated that the origin of *Herrickiceras* might lie in *Donenriquoceras* Wiedmann, 1960, or in *Imlayiceras*. In this regard, it has been observed in the Iberian Trough that the first occurrence of *Wrightoceras* is slightly below the one of *Donenriquoceras*, and this fact seem to rule out the possibility that the former group is derived from the latter.

Occurrence: It has been cited from lower to middle Turonian of North-Africa, Nigeria, Gabon, Spain, Middle-East, Oman, the USA, Mexico and South-America. In the Iberian Trough, a member of this genus has been identified in the *Spathites (Ingridella) malladae* subzone of the Central Sector. The remaining specimens come from the *Wrightoceras munieri* subzone and middle Turonian levels of the same region.

Wrightoceras llarenai (Karrenberg, 1935)
Fig. 10(1, 2)

1935. *Pseudotissotia llarenai* – Karrenberg, p. 143, Pl. 31, Fig. 14; Pl. 33, Fig. 14.

1950. *Pseudotissotia llarenai* Karrenberg – Bataller, p. 132 [included an un-numbered figure].

1960. *Wrightoceras llarenai* (Karrenberg) – Wiedmann, p. 720.

1964. *Wrightoceras llarenai* (Karrenberg) – Wiedmann, p. 114.

1978. *Wrightoceras llarenai* (Karrenberg) – Wiedmann and Kauffman, p. 3.

Type: Karrenberg (1935) described two specimens, figuring only the number I and did not designate a holotype.

Material and dimensions:

	D	*H* (%)	*B* (%)	*U* (%)
CA-S-399	706	332 (47)	256 (36)	135 (19)

Description: Compressed and involute ammonite, with weak ornamentation and subtrapezoidal whorl section. Tabulate ventral region limited by flat or slightly convex flanks, and deep and moderately narrow umbilicus with vertical walls. It shows six to eight weak umbilical tubercles per whorl that give rise to the same number of slender plications. Between each pair of these grow two or even more intercalated accessory plications. The small and elongated ventrolateral tubercles are

Fig. 10. 1, 2. *Wrightoceras llarenai* (Karrenberg, 1935), spécimen CA-S-399, de la sous-zone à *Spathites (Ingridella) malladae* de Condemios, × 1. 1. Vue ventrale. 2. Vue latérale. 3, 4. *Wrightoceras munieri* (Pervinquière, 1907), spécimen FT-R-818, de la sous-zone à *Wrightoceras munieri* de Fuentetoba, × 1. 3. Vue ventrale. 4. Vue latérale. 5. *Wrightoceras submunieri* Wiedmann, 1975b, spécimen TA-R-651, d'un niveau Turonien moyen inconnu de Condemios, vue latérale, × 1. 6, 7. *Donenriquoceras forbesiceratiforme* Wiedmann, 1960, spécimen PU-S-371, de la zone à *Mammites nodosoides* de Puentedey, × 1. 6. Vue ventrale. 7. Vue latérale. 8, 9. *Donenriquoceras forbesiceratiforme* Wiedmann, 1960, spécimen PU-S-381, du sommet de la zone à *Spathites (Ingridella) malladae* de Puentedey, × 1. 8. Vue latérale. 9. Vue aperturale.

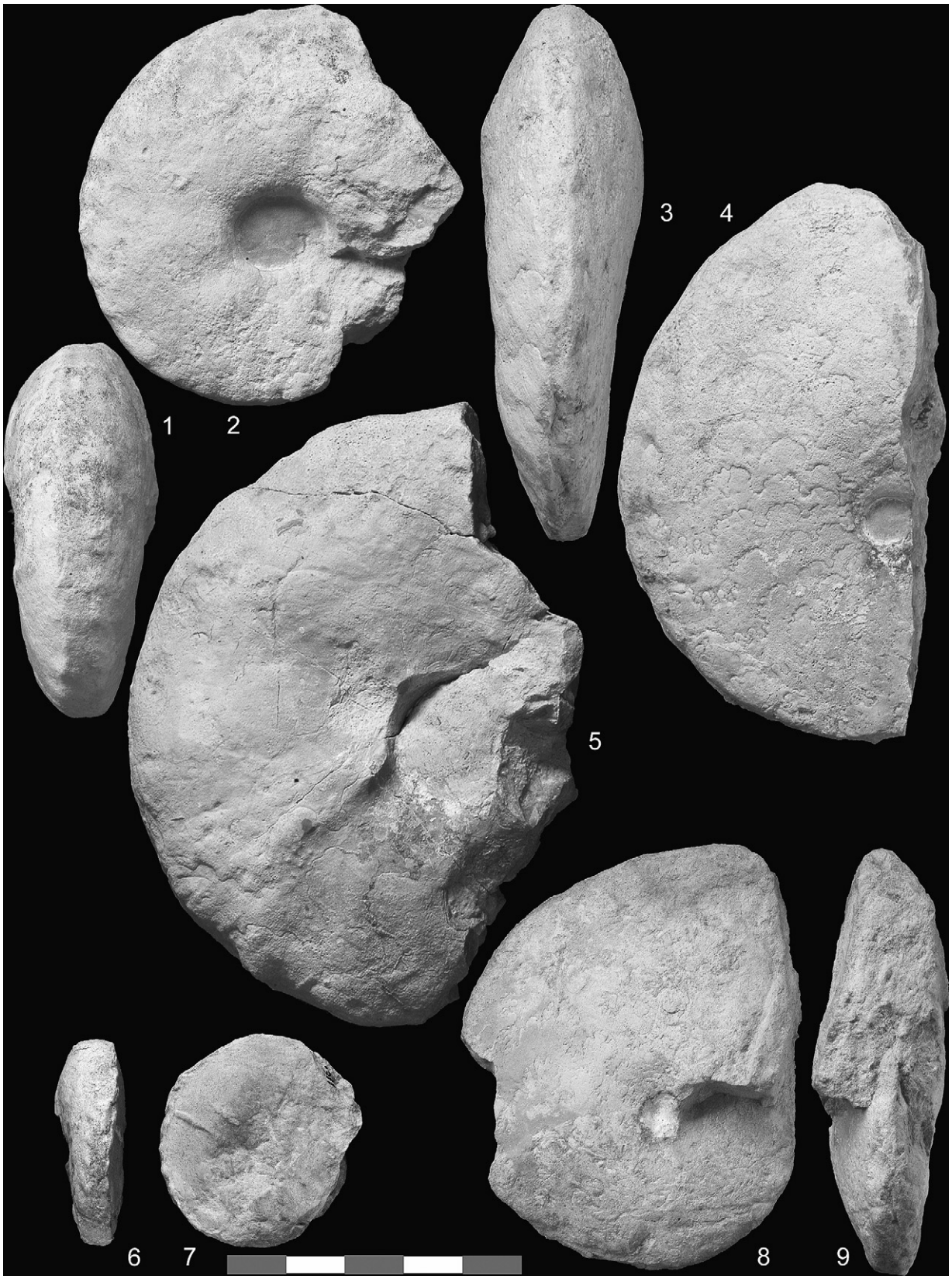

Fig. 10. 1, 2. *Wrightoceras llarenai* (Karrenberg, 1935), specimen CA-S-399, from the *Spathites (Ingridella) malladae* subzone of Condemios, × 1. 1. Ventral view. 2. Lateral view. 3, 4. *Wrightoceras munieri* (Pervinquière, 1907), specimen FT-R-818, from the *Wrightoceras munieri* subzone of Fuentetoba, × 1. 3. Ventral view. 4. Lateral view. 5. *Wrightoceras submunieri* Wiedmann, 1975b, specimen TA-R-651, from an unknown middle Turonian level of Condemios, lateral view, × 1. 6, 7. *Donenriquoceras forbesiceratiforme* Wiedmann, 1960, specimen PU-S-371, from the *Mammites nodosoides* zone of Puentedey, × 1. 6. Ventral view. 7. Lateral view. 8, 9. *Donenriquoceras forbesiceratiforme* Wiedmann, 1960, specimen PU-S-381, from the top of the *Spathites (Ingridella) malladae* zone of Puentedey, × 1. 8. Lateral view. 9. Apertural view.

perched on the plications, disposed parallelly to the direction of the growth. Ornamentation disappears on the ventral region. The suture line is quite simple for this genus.

Discussion: The ammonite of Karrenberg (1935) and the one presented herein are the only illustrated specimens of *W. llarenai*. Due to the rarity of this species, it has not conveniently been compared with other representatives of the genus. Among them, *W. wallsi* (Reyment, 1954) presents a notably depressed shell. *W. munieri* (Pervinquière, 1907) develops more involute coiling, with smaller umbilicus, a fairly smooth surface and a more complex suture line. *W. reymenti* Amard et al., 1981, has some striking ventrolateral grooves that slightly resemble those of *C. (C.) securiforme* (Eck, 1909), whereas *W. gagnieri* (Faraud, 1951) bears approximately 30 ribs per whorl and an oval whorl section. *W. submunieri* Wiedmann, 1975b, occurs above and has a more involute coiling and a slightly more complex suture line.

The presence of ornamentation, the relatively simple suture line and the early temporal distribution for the group reveal that *W. llarenai* can be considered one of the oldest and most primitive forms of *Wrightoceras*.

Occurrence: It is an endemic species of the Spanish lower Turonian. The specimens identified prior to this investigation come from the zone 4, also named of *Mammites revelierеanus*, of Karrenberg and from the zone T IV of Wiedmann in the North-Ebro Area. Both are biostratigraphic units that approximately coincide with the *Spathites (Ingridella) malladae* zone. The ammonite presented herein has been found in the *Spathites (Ingridella) malladae* subzone of Condemios, in the Guadarrama Area.

Wrightoceras munieri (Pervinquière, 1907)
Fig. 10(3, 4)

cf. 1897. *Discoceras* cf. *largilliertianum* d'Orbigny – Peron, p. 40, Pl. 14(1), Figs. 6, 7 .

1907. *Hoplitoides munieri* – Pervinquière, p. 217, Pl. 10, Figs. 1, 2; Text-Fig. 83.

?1921. *Hoplitoides munieri* Pervinquière – Chudeau, p. 467, Fig. 3.

non 1954. *Hoplitoides* cf. *H. munieri* Pervinquière – Kummel and Decker, p. 317, Pl. 33, Figs. 1, 2; Text-Figs. 7, 10.

?1956. *Hoplitoides inca* – Benavides-Cáceres, p. 475, Pl. 63, Figs. 6–11; Text-Fig. 54a, b.

1960. *Wrightoceras munieri* (Pervinquière) – Wiedmann, pp. 711–712, 721.

cf. 1960. *Wrightoceras* cf. *munieri* (Pervinquière) – Wiedmann, p. 712 [only].

1964. *Wrightoceras munieri* (Pervinquière) – Wiedmann, pp. 109, 111, 115.

cf. 1964. *Wrightoceras* cf. *munieri* (Pervinquière) – Wiedmann, p. 111 [only].

?1967. *Imlayiceras washbournei* – Leanza, p. 198, Pl. 4, Figs. 1–4; Pl. 6, Figs. 1, 4–6.

1975a. *Wrightoceras munieri* (Pervinquière) – Wiedmann, p. 24.

1975b. *Wrightoceras munieri* (Pervinquière) – Wiedmann, p. 144, Pl. 2, Fig. 2.

1978. *Wrightoceras munieri* (Pervinquière) – Wiedmann and Kauffman, p. 2.

1979. *Wrightoceras munieri* (Pervinquière) – Wiedmann, pp. 205, 209.

?1979. ?*Imlayiceras ralphimlayi* – Etayo-Serna, p. 88, Pl. 13, Fig. 3; Text-Fig. 8a.

1982. *Hoplitoides munieri* Pervinquière – Renz, p. 100, Pl. 31, Figs. 3a, b, 4a, b, 6a, b, 11a, b.

cf. 1982. *Hoplitoides* cf. *munieri* Pervinquière – Renz, p. 100, Pl. 31, Fig. 5a, b.

cf. 1982. *Wrightoceras* cf. *munieri* (Pervinquière) – Chancellor, p. 119, Figs. 24, 60–63.

1982. *Wrightoceras munieri* (Pervinquière) – Carretero-Moreno, p. 268.

1987. *Wrightoceras munieri* (Pervinquière) – Kennedy et al., p. 58, Pl. 10, Figs. 9–11; Text-Figs. 2e, ?11.

cf. 1987. *Wrightoceras* cf. *munieri* (Pervinquière) – Zaborski, p. 51, Figs. 38a, b, ?40.

1990. *Wrightoceras munieri* (Pervinquière) – Zaborski, Figs. 29, 30.

1994. *Wrightoceras munieri* (Pervinquière) – Chancellor et al., p. 96, Pl. 26, Figs. 1, 5, 8; Pl. 28, Figs. 1, 4; cf. Pl. 28, Figs. 2, 3; Pl. 29, Figs. 3–8; Pl. 36, Figs. 1, 2; Text-Figs. 18g, h, 19h, i.

1997. *Wrightoceras munieri* (Pervinquière) – Wiese, Pl. 3, Figs. 4, 5.

cf. 2003. *Wrightoceras* cf. *munieri* (Pervinquière) – Meister et al., p. 345, Pl. 2, Fig. 2.

Type: The holotype is the original of Pervinquière (1907: p. 217, Pl. 10, Fig. 2), from the Lower Turonian of Draa el Miaad, in Tunisia. After having been held in the SP and the UPMC, it is now kept in the MNHN with the number J04262.

Material and dimensions:

	D	*H* (%)	*B* (%)	*U* (%)
CG-R-514	687	328 (48)	161 (23)	121 (18)
FS-R-794		690	332	rv110
FT-R-818	998	569 (57)	293 (29)	85 (9)
FT-R-845				
FV-R-844	815	460 (56)	185 (23)	76 (9)
PS-R-272	459	240 (52)	165 (36)	50 (11)

Description: Very compressed or involute discoidal forms with subogival whorl sections truncated by narrow, sulcate and bicarinate venters that become tabulate or slightly arched during ontogeny. The flanks are slightly convex on their inner part, where they reach the greatest breadth, and convergent flat or convex on their outer part. The umbilici are relatively small, with vertical walls, and narrow and blunted margins. Suture lines with scarce secondary elements and relatively broad and simple saddles.

Discussion: The typical shell of this species is compressed and has a less concave venter than *Wrightoceras wallsi* (Reyment, 1954), lacking the radial plications that characterize *W. submunieri* Wiedmann, 1975b. Furthermore, *W. llarenai* (Karrenberg, 1935) shows a more depressed whorl section that resembles that of *W. wallsi* and has ribs disappearing as they

reach the ventrolateral angle. The shell of *W. reymenti* Amard et al., 1981, also exhibits a coarser shape, with a proportionally greater breadth than *W. munieri*.

Reyment (1954), Benavides-Cáceres (1956), Barber (1957), Wiedmann (1975b) and Zaborski (1987) were in agreement when considering *Hoplitoides mirabilis* Pervinquière, 1907, a probable synonym of *W. munieri*, differing from this species only in some details concerning the suture line or the breadth of the venter. Kummel and Decker (1954), however, indicated that they distinguished *H. mirabilis* without any difficulties by virtue of the deeper incisions presented on the first lateral saddle and lobe. Freund and Raab (1969) and Chancellor (1982) considered that *H. mirabilis* could be a homoeomorph coilopoceratid of *W. munieri*. Kennedy et al. (1987) excluded *H. mirabilis* from the synonymy of *W. munieri*, but included within it, nevertheless, the species *H. inca* Benavides-Cáceres, 1956, and ?*Imlayiceras ralphimlayi* Etayo-Serna, 1979, and although doubtful, *Proplacenticeras zeharense* Collignon, 1966, and *I. washbournei* Leanza, 1967. Chancellor et al. (1994) basically concurred with the observations made by Kennedy et al. (1987). They designated the lectotype of *H. mirabilis* and, after studying the features of *I. washbournei* and ?*I. ralphimlayi*, they considered that these two Colombian forms may probably be synonyms of *W. munieri*.

Regarding the possibility that *W. munieri* and *H. mirabilis* could be conspecific, after comparing the types of both taxa in the MNHN we have verified that, although their morphologies are so similar that it would be virtually impossible to differentiate *W. munieri* and *H. mirabilis* only on the basis of this feature, their suture lines are notably different. Similarly, in the Iberian Trough it has been observed that *W. munieri* and *H. mirabilis* have slightly different geographical and temporal distributions. We therefore have reached the conclusion that *W. munieri* and *H. mirabilis* are two homoeomorph species that should be assigned to different genera. In addition, the specimens of *H. inca* presented by Benavides-Cáceres (1956) develop morphologies easily assignable to *W. munieri*. In the same way, *I. washbournei* seems to be a mere synonym because, although the holotype of the taxon of Leanza presents feeble umbilical tubercles on the first whorls that disappear quite soon, their remaining features notably resemble the typical ones of *W. munieri*. The morphology of ?*I. ralphimlayi* is precisely the same as that of characteristic *W. munieri* but, as its suture line is unknown, it seems to be more reasonable to maintain the taxon of Etayo-Serna as a possible synonym. Likewise, in this species could be included some specimens that soon loose the tabulate venter and develop a wide and rounded body chamber, like the ammonites presented by Chudeau (1921) and Zaborski (1987: Fig. 40). Unfortunately, the specimens of *P. zeharense* of Collignon (1966) are too poorly preserved for a definite taxonomic determination, although they slightly remind of *W. munieri*.

Cobban and Hook (1980) considered that the specimens classified as *H.* cf. *H. munieri* by Kummel and Decker (1954) belong to the species *Herrickiceras costatum* (Herrick and Johnson, 1900). This opinion was also shared by Kennedy et al. (1987) and Chancellor et al. (1994), authors who observed that the specimens of Kummel and Decker (1954) have ribs, and own first lateral saddles, which are much wider than the first lateral lobes. These features certainly coincide with those of *H. costatum*. Chancellor et al. (1994) also refigured the ammonite classified as *Discoceras* cf. *largilliertianum* d'Orbigny by Peron (1897: p. 40, Pl. 14(1), Figs. 6, 7) that was included in the synonymy of *W. munieri* by these authors. Although no suture lines of this specimen can be observed, the similarities between it and the holotype of Pervinquière are certainly significant.

Occurrence: This species has been found in the lower Turonian of Tunisia, Spain, Venezuela, the USA and, possibly, Algeria, the Sudan, Peru, Colombia, Mexico, Nigeria and Gabon. Within the Iberian Trough, the species *W. munieri* is relatively common in the eponymous subzone of the Central Sector.

Wrightoceras submunieri Wiedmann, 1975b
Fig. 10(5)

1960. *Wrightoceras* cf. *munieri* (Pervinquière) – Wiedmann, p. 711 [only].

1964. *Wrightoceras* cf. *munieri* (Pervinquière) – Wiedmann, p. 109 [only].

1975a. *Wrightoceras* cf. *munieri* (Pervinquière) – Wiedmann, p. 25, Fig. 6a–c.

1975b. *Wrightoceras submunieri* – Wiedmann, p. 145, Pl. 3, Fig. 1.

1978. *Wrightoceras submunieri* Wiedmann – Wiedmann and Kauffman, Pl. 8, Fig. 2a–c.

1979. *Wrightoceras submunieri* Wiedmann – Wiedmann, Pl. 8, Fig. 2a–c.

Type: The holotype is specimen 1471/2 of the GPI, from the middle Turonian of Picofrentes, in the La Demanda Area of the Iberian Trough, Spain.

Material and dimensions:

	D	*H* (%)	*B* (%)	*U* (%)
FT-R-817	776	380 (49)	333 (43)	169 (22)
PS-R-270		371	318	rv120
TA-R-651	1118	510 (46)	414 (37)	230 (21)

Description: Compressed and involute ammonites with subtrapezoidal sections. Tabulate ventral regions and narrow umbilici with subvertical walls. The flat or moderately arched flanks can turn slightly concave near the ventral regions, and reach their greatest breadth close to the umbilical margins. Ornamentation consists of about ten radial plications per whorl that grow from the ventral regions, extending across the flanks and finally disappearing as they reach the ventrolateral margins.

Discussion: The ribbing of this species is very characteristic and allows differentiating it quite easily from the remaining forms of the genus. Moreover, *W. wallsi* Reyment, 1954, has a proportionally wider whorl, whereas the section of *W. munieri* (Pervinquière, 1907) is significantly more compressed and slightly more involute. *W. llarenai* (Karrenberg, 1935) presents less ribs per whorl, a wider umbilicus and a simpler suture line.

Occurrence: Until now, *W. submunieri* has only been identified in the middle Turonian of Spain, specifically in

Fuentetoba, in the La Demanda Area of the Iberian Trough. Wiedmann and Kauffman (1978) and Wiedmann (1979) proposed this species as index of their middle Turonian zone T IV.

Donenriquoceras Wiedmann, 1960

Type species: *Donenriquoceras forbesiceratiforme* Wiedmann, 1960, by original designation.

Diagnosis: Very involute and discoidal shells with whorl sections much higher than wide, narrow umbilici, sharp venters and flat or slightly convex flanks. The juvenile specimens possess flattened narrow venters and small elongated ventrolateral tubercles disposed obliquely to the direction of coiling. However, they soon disappear and adults are characterized by the total absence of ornamentation. The suture lines have five strongly marked lobes on the flanks, rounded saddles and bifid, asymmetric and deep lateral lobes.

Discussion: The genus can easily be differentiated from *Hoplitoides* von Koenen, 1898, and *Wrightoceras* Reyment, 1954, by the form of the shell and the complexity of the suture line of the group of Wiedmann. It can also be distinguished from homoeomorph species of *Neoptychites* Kossmat, 1895, by the ornamentation and the appearance of the first lateral saddle, and from the representatives of *Eotissotia* Barber, 1957, by the suture line and the presence of juvenile ventrolateral tubercles. Likewise, the absence of a keel as well as the deep lateral lobe, among other features, make it possible to differentiate this genus from *Choffaticeras* Hyatt, 1903.

Regarding its phylogeny, Wiedmann (1960, 1964) indicated that *Donenriquoceras* is a cryptogenetic taxon. Years later, after proposing the new group *Herrickiceras*, Cobban and Hook (1980) pointed out that *Donenriquoceras* and *Imlayiceras* Leanza, 1967, might be possible ancestors of their genus. At present, *Herrickiceras* and *Imlayiceras* are generally considered synonyms of *Wrightoceras*. The supposition of Cobban and Hook (1980), therefore, is already indicative of a close relationship between *Wrightoceras* and *Donenriquoceras*. In the present investigation, it has been observed that during the earliest ontogenetic stages the members of this genus maintain subtabulate venters flanked by small ventrolateral tubercles that disappear soon with growth. These features, also presented by the small specimen of Wiedmann (1960: Pl. 7, Figs. 3, 4), match closely with typical ones of juvenile members of *Wrightoceras*. This fact confirms the great phylogenetic proximity between both genera. In the same way, the slightly earlier appearance of the Reyment's group seems to indicate that the origin of *Donenriquoceras* is in *Wrightoceras*.

Occurrence: This genus, monospecific until now, has only been identified in the lower Turonian of Spain, as is detailed below.

Donenriquoceras forbesiceratiforme Wiedmann, 1960

Fig. 10(6–9)

1960. *Donenriquoceras forbesiceratiforme* – Wiedmann, pp. 711, 723, 758, Pl. 5, Fig. 3; Pl. 7, Figs. 1–4; Text-Figs. 13, 14.

1964. *Donenriquoceras forbesiceratiforme* Wiedmann – Wiedmann, pp. 109, 116, 142, Figs. 30a–c, 31a, b; Text-Figs. 32, 33.

1975a. *Donenriquoceras forbesiceratiforme* Wiedmann – Wiedmann, p. 24.

1975b. *Donenriquoceras forbesiceratiforme* Wiedmann – Wiedmann, p. 140.

1978. *Donenriquoceras forbesiceratiforme* Wiedmann – Wiedmann and Kauffman, p. 2.

1979. *Donenriquoceras forbesiceratiforme* Wiedmann – Wiedmann, pp. 189, 193, 209.

1984. *Choffaticeras forbesiceratiforme* (Wiedmann) – Meléndez-Hevia, p. 108, Pl. 13, Fig. 1a, b.

1991. *Donenriquoceras forbesiceratiforme* Wiedmann – Santamaría-Zabala, p. 161, Pl. 9, Fig. 7.

1996. *Donenriquoceras forbesiceratiforme* Wiedmann – Wright in Kaesler, p. 179, Text-Fig. 138/3a–c.

Type: The holotype is specimen CE 1162/5 of the GPI, illustrated by Wiedmann (1960: Pl. 5, Fig. 3; Pl. 7, Figs. 3, 4; Text-Fig. 13).

Material and dimensions:

	D	*H* (%)	*B* (%)	*U* (%)
CA-R-76	1212	640 (53)	352 (29)	106 (9)
FV-R-72	1284	rv708 (55)	422 (33)	rv100 (8)
PU-S-239	614	328 (53)	rv70 (11)	45 (7)
PU-S-371	375	194 (52)	120 (32)	31 (8)
PU-S-381	750	448 (60)	rv227 (30)	67 (9)
PU-S-383	rv770	rv450 (58)	rv145 (19)	rv65 (8)
PU-S-422	rv935	rv500 (53)	rv125 (13)	rv91 (10)

Description: Discoidal and involute forms with suboval compressed whorl sections and smooth, slightly convex flanks, reaching their greatest breadth close to the umbilical borders. Narrow and slightly arched or rounded venters, and small umbilici with blunted margins. Feeble ventrolateral tubercles that disappear during early ontogenetic stages may appear on the first whorls. The suture lines present the typical bifid and asymmetrical lateral lobes of the genus.

Discussion: This species has a very characteristic whorl section that in some occasions may, however, be hard to distinguish from some members of the genera *Choffaticeras* and *Neoptychites*. To differentiate *D. forbesiceratiforme* from *C. (C.) quaasi* (Peron, 1904) and *C. (C.) pavillieri* (Pervinquière, 1907) it is very useful to consider that the venter of the former species is somewhat broader and more rounded. Likewise, *D. forbesiceratiforme* lacks constrictions and presents a tabulate ventral region flanked by tiny ventrolateral tubercles during the first ontogenetic stages, and does not develop lateral bulges on the adult body chamber, in contrast to *N. cephalotus*.

Occurrence: This is a species endemic to the lower Turonian of Spain, occurring in the top of the *Choffaticeras (Leoniceras) luciae* subzone and in the *Mammites nodosoides* zone of the Inner Castilian Platform.

5. Conclusions

In the present work have been described new specimens assigned to the species *Pseudotissotia* sp., *Choffaticeras*

(Choffaticeras) quaasi, *C. (C.) pavillieri*, *C. (C.) segne*, *C. (C.) sinaiticum*, *C. (Leoniceras) luciae*, *C. (L.) barjonai*, *Wrightoceras llarenai*, *W. munieri*, *W. submunieri* and *Donenriquoceras forbesiceratiforme*. Among these species, *C. (C.) sinaiticum* had never previously been mentioned in the Iberian Trough. During the revision, has been noticed the presence of specimens which are attributable to *Thomasites koulabicus*, *T. meslei*, *W. wallsi*, *C. (C.)* cf. *meslei*, *C. (L.) massipiana*, *C. (L.) philippi* and, possibly, *C. (C.) douvillei* in the collections of the GPI and the UCM. Moreover, some specimens of *T.* cf. *rollandi* and *T.* sp. gr. *gongilensis-koulabicus* have both been properly figured by Santamaría-Zabala (1991, 1995). Therefore, it can be assumed that the Pseudotissotiidae are represented by the genera *Thomasites*, *Pseudotissotia*, *Choffaticeras*, *Wrightoceras* and *Donenriquoceras* in the Iberian Trough, where the species *T. koulabicus*, *T.* cf. *rollandi*, *T.* sp. gr. *gongilensis-koulabicus*, *T. meslei*, *W. wallsi*, *Pseudotissotia* sp., *C. (C.)* cf. *meslei*, *C. (C.) quaasi*, *C. (C.) pavillieri*, *C. (C.) segne*, *C. (C.) sinaiticum*, *C. (L.) luciae*, *C. (L.) barjonai*, *C. (L.) massipiana*, *C. (L.) philippi*, *W. llarenai*, *W. munieri*, *W. submunieri*, *D. forbesiceratiforme* and, probably, *C. (C.) douvillei* have been properly identified.

Furthermore, the distribution of the new members of the Pseudotissotiidae presented here has been determined (Fig. 11). The records of its representatives have been obtained from lower and middle Turonian levels of the Iberian Trough. *Choffaticeras (Choffaticeras)* has been identified from the *Choffaticeras (Choffaticeras) quaasi* zone to the *Spathites (Ingridella) malladae* subzone. Among its species, *C. (C.) quaasi* is the first species of the genus and, possibly, of the family established in this palaeogeographical region. Its specimens have been obtained from the eponymous subzone. The levels from the base of the lower Turonian have also probably provided one specimen of *Pseudotissotia* sp. Although the distribution of the species *C. (C.) segne* could not be determined precisely, it seems to comprise the *Choffaticeras (Choffaticeras) quaasi* zone and the *Spathites (Ingridella) malladae* subzone. *C. (C.) pavillieri* has been identified in the upper part of the *Choffaticeras (Choffaticeras) quaasi* zone and in the *Spathites (Ingridella) malladae* subzone. *C. (C.) sinaiticum*, the last species assigned to the subgenus registered in the Iberian Trough, has been obtained from the upper part of the *Spathites (Ingridella) malladae* subzone. On the other hand, *C. (L.) luciae* and *C. (L.) barjonai*, the main representatives of *Choffaticeras (Leoniceras)* have been collected from the lower and from the upper part of the *Choffaticeras (Leoniceras) luciae* subzone, respectively. With regard to *Wrightoceras*, although one member of this genus, attributed to *W. llarenai*, has been found in the *Spathites (Ingridella) malladae* subzone, its continuous records have been obtained in the *Wrightoceras munieri* subzone and in middle Turonian levels. *W. munieri* has been identified in the eponymous subzone and specimens of *W. submunieri* have been collected from the middle Turonian. The only species of *Donenriquoceras* obtained, *D. forbesiceratiforme*, has been located in the top of the *Choffaticeras (Leoniceras) luciae* subzone and in the *Mammites nodosoides* zone. Therefore, the last specimens belonging to the genus *Wrightoceras* can be considered as the last members of Pseudotissotidae in the Iberian Trough.

In terms of the phylogeny of the group, have been identified two possible evolutionary lineages, one of them joining *C. (C.) quaasi*, *C. (C.) pavillieri* and *C. (C.) sinaiticum*, within the subgenus *C.* (*Choffaticeras*), and *C. (L.) luciae* and *C. (L.) barjonai* within the subgenus *C.* (*Leoniceras*) (Fig. 11). Their members initially tend to develop progressively more involute, compressed and sharpened forms, but subsequently lose the ventrolateral keels and become more evolute and depressed. The second evolutionary lineage joins *W. munieri* and *W. submunieri*, and it is characterized by the tendency to increase

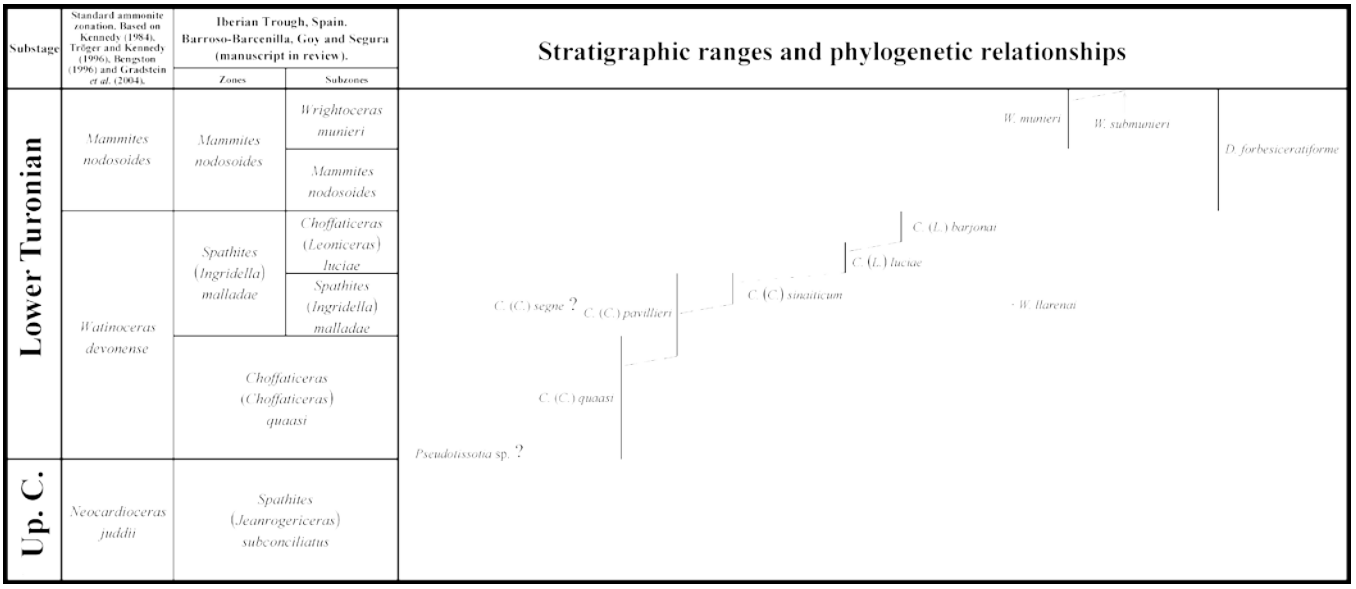

Fig. 11. Stratigraphical ranges of the identified species of Pseudotissotiidae and their suggested phylogenetic relationships.
Fig. 11. Extension stratigraphique des espèces de Pseudotissotiidae identifiées dans ce travail avec leurs relations phylogénétiques possibles.

the relative whorl breadth and the umbilical width as well as to develop plications. *Wrightoceras* possibly gave rise to the genus *Donenriquoceras*.

After observing the distribution of the family in the Iberian Trough, four main phases can be distinguished. These are characterized by the successive dominance of *C.* (*Choffaticeras*), *C.* (*Leoniceras*), *Donenriquoceras* and *Wrightoceras* with *Donenriquoceras* (Fig. 12). The first one has been identified in the *Choffaticeras (Choffaticeras) quaasi* zone and the *Spathites (Ingridella) malladae* subzone, and during this phase *C.* (*Choffaticeras*) is mainly represented by tricarinate species of *Choffaticeras*, such as *C. (C.) quaasi*, *C. (C.) pavillieri*, *C. (C.) segne* and *C. (C.) sinaiticum*. They are morphologies considered as primitive as they show great similarities with *Pseudotissotia*, one of the earliest genera of the family. The second phase, that of *C.* (*Leoniceras*), has been registered in the *Choffaticeras (Leoniceras) luciae* subzone. In this phase, the most widespread forms of the family are monocarinate and, therefore more evolved, like *C. (L.) luciae* and *C. (L.) barjonai*. The third phase, named of *Donenriquoceras*, has been identified in the *Mammites nodosoides* subzone. During this phase *D. forbesiceratiforme*, the only species of *Donenriquoceras*, represents the Pseudotissotiidae. Finally, the phase of *Wrightoceras* with *Donenriquoceras*, the fourth and last one, has been registered in the *Wrightoceras munieri* subzone. In this phase, members of the family belong mainly to *Wrightoceras*, specifically to *W. munieri*, and secondary to *Donenriquoceras*, specifically to *D. forbesiceratiforme*. These four phases seem not only to coincide with the evolutionary intervals followed by the family in other palaeogeographical regions, but also by many other groups. Each phase seems to have been mainly caused by different palaeoenvironmental circumstances, conditioned by important changes taking place worldwide in all oceans during the late Cenomanian and early Turonian, as will be detailed by the authors of this paper shortly.

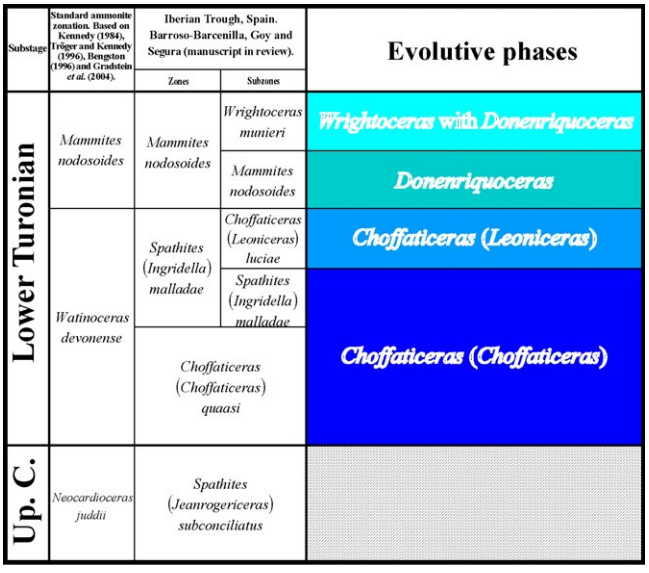

Fig. 12. Observed evolutive phases in the evolution of the family Pseudotissotiidae in the Iberian Trough.

Fig. 12. Phases évolutives observées pour l'évolution de la famille Pseudotissotiidae dans le Bassin Ibérique.

Acknowledgements

The first author appreciates the help offered by Dr Alexander Liebau and Dr Hartmut Schulz from the Institut und Museum für Geologie und Paläontologie of the Universität Tübingen, Germany, by Prof. Dr Miguel Brandão and Mrs. Joanna Pachucka from the Museu do Instituto Geológico e Mineiro of Lisboa, Portugal, and by Dr Annie Cornée, Dr Didier Merle, Dr Jean-Michel Pacaud and Prof. Dr Jean-Paul Saint Martin from the Muséum National d'Histoire Naturelle of Paris, France, in order to study the types from the upper Cenomanian and lower Turonian which are held in their respective institutions. He also expresses his gratitude to Prof. Dr William James Kennedy from the Oxford University Museum of Natural History, UK, and Prof. Dr Francis Amédro from Calais, France, for their valuable remarks concerning the identification of some of the specimens presented herein.

We would like to thank Prof. Dr Manuel Segura Redondo from the Universidad de Alcalá de Henares, Spain, for his help in lending us some cephalopods belonging to his own collection and for his useful information about the Spanish Upper Cretaceous. We also want to express our gratitude for the excellent work carried out by Mr. Ignacio Meléndez Hevia, who collected and analysed some of the specimens herein described while working on his final project for graduation. Likewise, we want to thank Mrs. María Inmaculada Martínez Martínez, graduate in English Philology, and Miss María del Mar Martínez Martínez, graduate in Translation and Interpretation, for their work as translators, as well as Mr. Carlos Alonso Recio, for his work as photographer for the Departamento de Paleontología of the Universidad Complutense de Madrid, Spain. We also recognize the work of the reviewers of this manuscript, Dr Herbert Christian Klinger from the South African Museum of Cape Town, South Africa, and Dr Christian Meister from the Muséum d'Histoire Naturelle de Genève, Switzerland, who have notably improved its original content.

This study has been carried out within the Project 01/1003/2001 of the Dirección General de Investigación of the Comunidad de Madrid, Spain, and the Project CGL 2005-01765/BTE of the Ministerio de Educación y Ciencia of Spain, and financed by these institutions and by the Social Fund of the European Union.

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